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THE UNIVERSITY OF ALBERTA

RESPONSES OF TAMARACK AND BLACK SPRUCE FORESTS TO DRAINAGE, THINNING AND FERTILIZATION OF ALBERTA PEATLANDS

BY

ANCELM GODFERY MUGASHA ©

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH IN
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DEGREE OF DOCTOR OF PHILOSOPHY

IN

FOREST SOILS

DEPARTMENT OF SOIL SCIENCE

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DEDICATION

To my father the late Godfrey Kahwa Mugasha who taught me how to plough

and

to my mother Asteria Kahwa Mugasha who taught me how to plant.

ABSTRACT

Nutrient dynamics and foliar responses of tamarack (*Larix laricina* (Du Roi) K. Koch.) and black spruce (*Picea mariana* (Mill.) B.S.P.) to silvicultural manipulations of minerotrophic peatlands in Alberta, Canada were addressed in a series of field experiments. Ditch drainage, thinning and fertilization of forested peatlands in central Alberta were used to alter aeration, temperature and water relations of near-surface soil, and to increase nutrient availability and uptake in order to improve conifer productivity. Selected physiological processes (foliar nutrient dynamics, and carbon fixation and allocation to needles) and soil chemistry were studied in order to understand how these silvicultural manipulations might influence the trees.

Drainage lowered the water table, improved aeration and increased temperature of near-surface soil. This resulted in increased net assimilation rate, mesophyll conductance to CO_2 and foliar and needle litter nutrient concentrations, but had no effect on stomatal conductance or seasonal foliar nutrient patterns. However, drainage delayed bud flush in spring and needle senescence in fall. Drainage decreased unit needle mass of black spruce presumably due to preferential allocation of carbon to belowground. The unit needle mass of tamarack was not affected by drainage presumably due to initially favourable shoot/root ratio and less reliance of tamarack on soil mineral-N for current growth. Thinning increased foliar N and P and unit needle mass. Neither drainage nor thinning removed nutrient deficiencies that existed prior to application of treatments.

Nitrogen fertilization increased foliar N concentration and unit needle mass, but resulted in foliar nutrient imbalances for both species. Increased unit needle mass with N fertilization on the drained site is indicative of a reduced proportion of photosynthate that was allocated to belowground with high N availability.

A field experiment using ^{15}N-labelled urea fertilizer showed that about 50% of applied fertilizer was immobilized in soil, a low proportion was recovered in trees, a greater proportion of N taken up by trees was allocated to actively growing needles, twigs and roots, uptake by black spruce was much greater than that of tamarack, and recovery of N fertilizer increased during the second growing season for black spruce but not for tamarack.

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Chapter 1

GENERAL INTRODUCTION

1.1 INTRODUCTION

A gradual decline in productive forest land base in Alberta may be attributable partly to withdrawal for other land uses. To compensate for this trend, intensive management of forested peatlands is being contemplated since these peatlands already support the growth of commercially important tree species such as tamarack (*Larix laricina* (Du Roi) K. Koch.) and black spruce (*Picea mariana* (Mill.) B.S.P.).

The productivity of tamarack and black spruce in natural peatlands is very low (Dang and Lieffers 1989; Lieffers and Macdonald 1990; Humphrey 1990). This is due to poor soil aeration (Lahde 1969; Paivanen 1973; Campbell 1980; Mannerkoski 1985; 1991), low soil temperature (Lieffers 1988; Lieffers and Rothwell 1986, 1987) and low availability of nutrients (Macdonald and Lieffers 1990; Lieffers and Macdonald 1990; Humphrey 1990), all related to high water table.

Drainage of peatlands for forestry production in the USSR and in some Scandinavian countries has been carried out for over 100 years. In Finland, 5.7 million ha, about 50% of the total peatland area, had been drained for forestry by 1989 (Paivanen 1991). In Sweden, the corresponding area is 1.0 million ha, or 12% of the total (Hanell 1988, 1991) and in the USSR about 6.5 million ha (equivalent to 3%) have been drained (Vompersky 1991). In Canada, the potential for significant increase in tree growth and increasing productive land base through drainage have not been fully recognized. To date in Canada, fewer than 25,000 ha, less than 0.02% of the total peatland area, have been drained for forestry purposes, and these have been mainly on an experimental basis (Haavisto and Jeglum 1991).

Drainage of peatlands improves conifer growth (Payandeh 1973, 1982; Dang and Lieffers 1989; Lieffers and Macdonald 1990; Humphrey 1990). Drainage lowers the water table thereby improving soil aeration (Paivanen 1973; Campbell 1980; Mannerkoski 1985; 1991), increasing soil temperature and improving moisture regimes of surface layers of peatland soils (Lieffers 1988; Lieffers and Rothwell 1987; Rothwell 1991).

These, in turn, enhance microbial activity, organic matter decomposition and nutrient release (Williams 1974; Williams and Wheatley 1988; Paivanen 1991). Improved soil conditions also enhance root growth (Boggie 1972; Lieffers and Rothwell 1987; Zhang and Liu 1991), water and nutrient uptake (Shoulders and Ralston 1975; Glinski and Stepniewski 1985) and transport from roots to leaves as a result of increased transpiration (Smith *et al.* 1989).

Drainage of peatlands by means of open ditches does not lower the water table uniformly, but follows a mounding pattern (Boelter 1965), with maximum depth at ditch edges and minimum at the midpoints between ditches (Rothwell 1991). Lieffers and Rothwell (1987) observed differences of 5 to 40 cm in water table levels between ditch edge and midpoints in a drained fen in Central Alberta. In Ontario, temperatures at ditch edges averaged 2°C higher and volumetric moisture content within 30 cm depth was 13% lower at edges than at midpoint locations between ditches (Rothwell 1991). Similar trends have been observed in drained peatlands in central Alberta (Rothwell and Silins 1990). These variations in soil environment may result in variation in tree growth responses. Trottier (1991) observed that dbh and height growth of 20-year-old tamarack trees decreased with increasing distance from the edge of drainage ditch.

Conifer growth in drained organic soils is sometimes limited by low levels of available nitrogen, phosphorus and potassium (Humphrey 1990; Lieffers and Macdonald 1990; Wells 1991) and some micronutrients (Veijalainen 1977, Humphrey 1990). Fertilization could improve the productivity of such nutrient-poor forested peatlands because it provides a readily available nutrient source and may also enhance decomposition of organic matter. Fertilization for the purpose of increasing tree growth in drained boreal peatlands in Canada has been carried out experimentally (see Payandeh 1982; Stanek 1976; Zdancewicz 1987; Wells 1991). In Alberta one fertilizer trial site was established prior to 1987 (Hillman 1989). Because of current interest in improving productivity of forested peatland in Alberta, fertilization may be an essential forest management tool.

N-fertilization of drained peatlands has been shown to increase tree growth (Alban and Watt 1981; Payandeh 1982; Zdancewicz 1987;

Wells 1991). However, the tree uptake efficiency of and fate of applied fertilizer N in forested boreal peatland ecosystems in Western Canada are undocumented. Nason and Myrold (1991) observed that the use of labelled ^{15}N-fertilizers offer an opportunity for: a) identifying pathways of N movement in soil and plant, b) quantifying the fate and efficiency of N uptake, and c) calculating of gross rates of N transfers or transformations. For this thesis, ^{15}N labelled urea was used for fertilization of a tamarack/black spruce mixed stand on a drained minerotrophic peatland in order to gain some understanding of a) and b) above.

Fertilization of dense stands may result in increased growth of some trees that may *never* reach marketable size. Hence, thinning alone or with fertilization may be an essential forest management tool for dense stands. There is little quantitative information on the effect of thinning on tree growth in drained boreal peatlands (Hillman 1989). However, there exists some information on the effect of thinning of upland tree species (see Weetman 1968, 1971; Brix 1983; Lavigne 1988a,b, 1991). Response to thinning is a function of tree species, stand age, degree of thinning and stand site quality. In general, thinning increases foliage, stem- and branch-wood biomass (Brix 1981). Increased stem growth in thinned stands may be a result of both increased total foliar biomass and foliage efficiency (Kellomaki *et al.* 1982; Brix 1983; Mead *et al.* 1984). This is related to reduced stand density and thereby minimized competition, as well as increased soil water and soil temperature which in turn may enhance microbial activity and mineralization and uptake of nutrients. If these improvements occur in thinned stands, then increased foliar nutrients and subsequently, needle mass should result.

Drainage of peatlands may result in a rapid change in soil hydrological, physical (e.g. soil aeration, soil water availability, soil porosity, and bulk density) properties and a gradual change in chemical (especially nutrient cycling) and biological (macro- and micro-organism population and activity) properties. These changes in soil properties due to drainage may result in variation in tree growth response over time. In central Alberta, soil nutrient status, and peatland conifers' ecophysiological, nutritional and growth responses to drainage were evaluated several years after the lowering of the water table (see Dang and Lieffers 1989; Humphrey 1990; Lieffers and Macdonald 1990; Macdonald and Lieffers 1990). These studies suggest that drainage improves conifer nutrient relations and photosynthetic performance, and increases tree growth. However, there is no information on these same responses for conifers in recently drained peatlands. The goal of the research reported in this thesis was to fill a gap in the present knowledge on nutrient dynamics and tree growth response to drainage. Thinning and fertilization treatments were also superimposed on drainage to study the interaction effects of these treatments.

The effect of interactions of drainage and fertilization, or thinning and fertilization on growth of peatland conifers in western Canada is undocumented. Several years are required to assess stem growth responses to these treatments (see Dang and Lieffers 1989; Humphrey 1990). However, foliar responses measured within the first or a few years after imposing treatments may be interpreted as early indicators of subsequent stemwood growth response (Timmer and Stone 1978; Timmer and Morrow 1984; Waring and Schlesinger 1985). Implicit in this application is that: a) since the leaf is the focal point of many physiological functions in the tree, particularly photosynthesis, it serves as a sensitive indicator of productivity and subsequent stem growth, and b) growth effects from treatment induced changes in photosynthetic capacity and/or efficiency, are reflected earlier in the foliage than in stem growth, e.g. dbh, the more conventional location for measuring tree growth (Timmer and Morrow 1984; Zdancewicz 1987).

1.2 OBJECTIVES AND APPROACH

To understand how drainage, thinning and fertilization influence tamarack and black spruce productivity, I studied several physiological processes in trees; i.e. foliar nutrient accumulation, retranslocation and resorption, carbon fixation and allocation to foliage and other tree components, needle growth, and quality of needle litter.

In addition, I used ^{15}N-labelled urea fertilizer as a tool to study the dynamics and fate of applied N fertilizer.

The specific objectives of this study were to evaluate:

1. The effect of thinning and fertilization of a drained shallow minerotrophic peatland on foliar nutrient status and unit needle mass of black spruce.
2. The effect of drainage and fertilization of a minerotrophic peatland on foliar nutrient status, unit needle mass, photosynthesis and water relations, seasonal foliar nutrient patterns (accumulation, retranslocation and resorption) and quality of needle litter of tamarack and black spruce.
3. The effect of drainage of on some short term physical and chemical (nutritional) responses of peat of surface layers in a minerotrophic peatland soil.
4. The use of ^{15}N-urea fertilizer as a tool to: a) describe seasonal dynamics of fertilizer N in soil and foliage, b) describe the variation of fertilizer N with tree crown position and needle age, c) estimate fertilizer N distribution in aboveground tree components, and d) quantify the fate of urea fertilizer.

Three field experiments were carried out at two locations in central Alberta, Canada. The first experiment was established near Valleyview on a shallow peated soil to evaluate the effect of thinning and fertilization on foliar response of black spruce on drained (summer 1986) minerotrophic peatland. The other two experiments were established in spring of 1989 near Edson in a minerotrophic peatland drained in fall 1987. The second experiment was undertaken to evaluate the effect of drainage and fertilization on foliar and ecophysiological responses of tamarack and black spruce. The third experiment used ^{15}N-labelled urea fertilizer as a tool to evaluate seasonal pattterns, uptake efficiency, distribution and recovery of fertilizer N in a tamarack/black spruce ecosystem. With this approach I thought that an overall picture of the response to silvicultural intervention in the functioning of the peatland ecosystem would evolve.

The results are reported in chapters 2 through 9. Objective 1 is dealt with in chapter 2, objectives 2 and 3 are dealt with in chapters 3 through 7. Objective 4 is dealt with in chapters 8 and 9. The general discussion and conclusions (chapter 10) bring together the results presented in other chapters.

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Chapter 2

FOLIAR RESPONSES OF BLACK SPRUCE TO THINNING AND FERTILIZATION ON A DRAINED SHALLOW PEAT

2.1 INTRODUCTION

Information on conifer growth responses to combined thinning and fertilization on drained, boreal peatlands of western Canada is generally lacking. Recently, however, Hillman (1989) assessed the growth of 30-year-old black spruce in an unreplicated experiment on a minerotrophic, boreal peatland with 0.5 to 1.2 m of peat (Gleysols and Terric Fibric Mesisol; 56° 34' N, 111° 19' W) which had been drained and in which the stand had been thinned and fertilized ten years earlier. Neither thinning nor N or P fertilizers increased height growth in the drained area, but N did increase growth in the undrained area. Nitrogen and P fertilizers, when applied individually, and thinning alone resulted in significant root collar diameter growth in the drained area.

This chapter examines the effect of stand density control (thinning), fertilization, and distance from drainage ditches on needle mass and on foliar N, P and K concentrations and contents in the second growing season after thinning and fertilization of a 50- to 60-year-old black spruce stand on an experimentally-drained, thin organic soil. This stand was typical of a high priority candidate for commercial drainage and fertilization because it met the criteria set by the Peat and Peatlands Diversification and Innovation Symposium held in Quebec, Canada in 1989 (Jeglum 1991) that the most attractive sites for drainage for forestry are those that are already forested, and that have one or more of the following attributes: a) they already show moderately good growth, b) they are on shallow-peated sites so that drainage allows roots to exploit underlying mineral soil, c) they are already stocked with the

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A version of this chapter has been published.
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desirable species, and d) they are in mid rotation so that the time for carrying interest on the initial investment is relatively short.

2.2 MATERIALS AND METHODS

2.2.1 Study area

The study area in central Alberta (853 m a.s.l.; 54° 55' N, 116° 45' W., Fig. 2.1) is classified as a treed swamp (Hillman 1987) or an intermediate fen based on water chemistry (Sjors 1950). Prior to imposition of experimental treatments mean stand density, basal area, height and dbh were 6,580 stems.ha^{-1}, 15.8 m^{2}.ha^{-1}, 4.62 m, and 4.9 cm, respectively (Alberta Forest Service 1987). The ground vegetation consisted primarily of Labrador tea (*Ledum groenlandicum*) with some sedges (*Carex* spp.), *Sphagnum fuscum*, *S. angustifolium* and *S. magellanicum* (Hillman 1987).

The very poorly drained Gleysols and Terric Mesisols (Agriculture Canada Expert Committee on Soil Survey 1987) were characterized by a thin (30 to 60 cm, Appendix 11.1) peat over mineral soil ranging from silt loam and silty clay to clay texture, probably of a lacustro-till origin (Appendix 11.2). The slope of the area was 0.8%. Pedons sampled to 60 cm depth had low electrical conductivity ($\leq$ 0.2 dS m^{-1}), pH ranged between 4.4 and 6.3, the soil C/N ratio ranged from 27 to 130, and bulk density increased from 0.03 Mg m^{-3} at 5 cm depth to 1.61 Mg m^{-3} at 60 cm depth (Table 2.1).

Climatically, the study area is within the wet subregion of the boreal mixedwood ecoregion (Strong and Leggat 1981, Corns and Annas 1986). Monthly air temperatures and precipitation at the study area are compared with the 1951-80 means at Valleyview (762 m a.s.l.; 55° 4'N, 117° 16'W), 35 km to the northwest (Fig. 2.2). Annual air temperature and precipitation at Valleyview are respectively 2.3° C and 519 mm, with 33% as snow. June and July precipitation total about 150 mm. July and January air temperatures average 16° C and -16° C, respectively. The average frost free period is 100 days with 2,000 growing degree days through September (Hillman 1987).

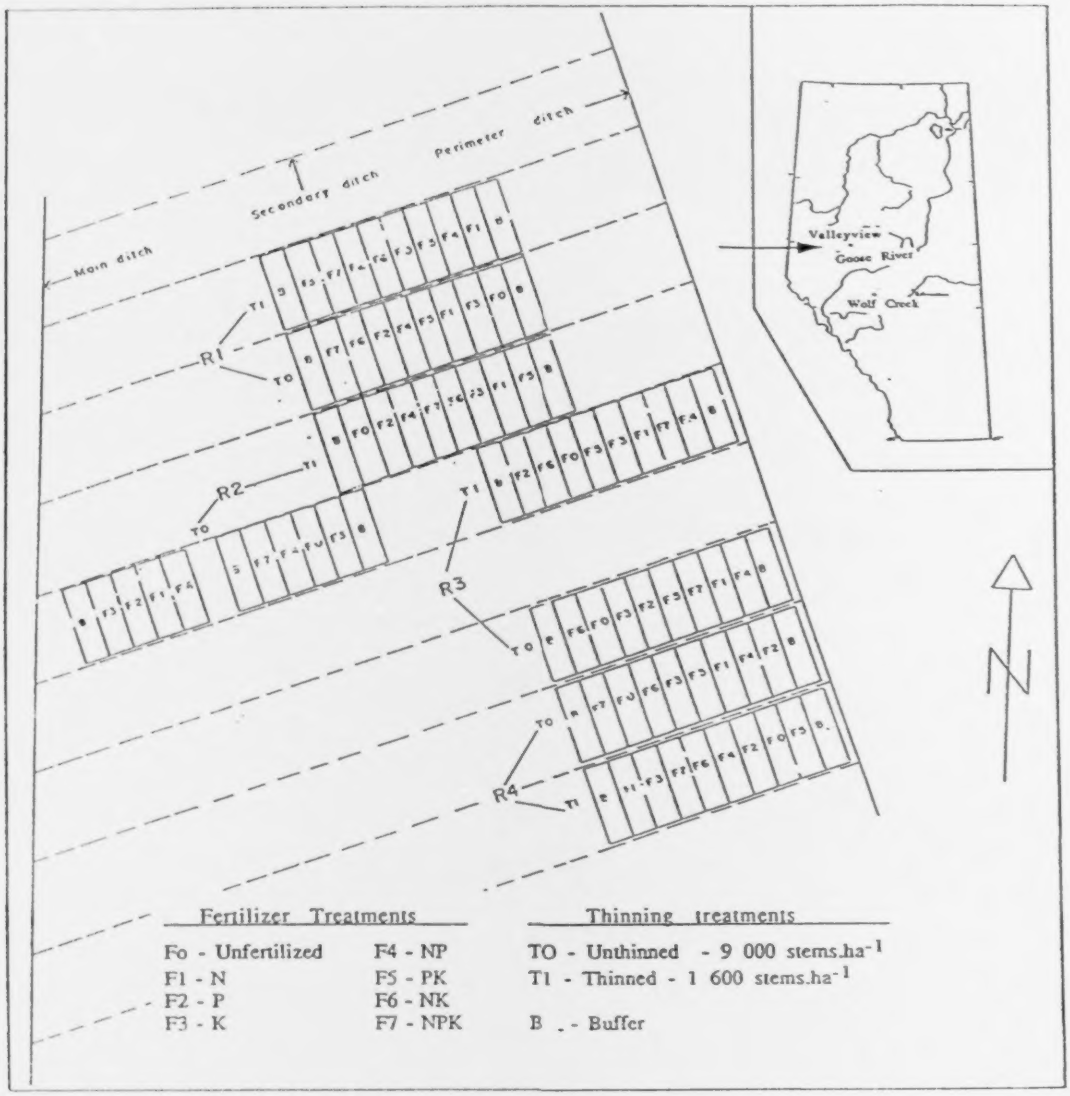

Main ditch
Secondary ditch
Perimeter ditch
R1
R2
R3
R4
T1
TO
Valleyview
Goose River
Wolf Creek
N
Fertilizer Treatments
Fo - Unfertilized
F1 - N
F2 - P
F3 - K
F4 - NP
F5 - PK
F6 - NK
F7 - NPK
Thinning treatments
TO - Unthinned - 9 000 stems.ha⁻¹
T1 - Thinned - 1 600 stems.ha⁻¹
B - Buffer

Figure 2.1: Location and layout of the thinning-fertilization experiment at Goose River Wetland Drainage Project, central Alberta (Alberta Forest Service 1987). Insert - map of Alberta. The area was ditched during summer 1986, thinned in March/April 1987 and fertilized on 8-9 June 1987.

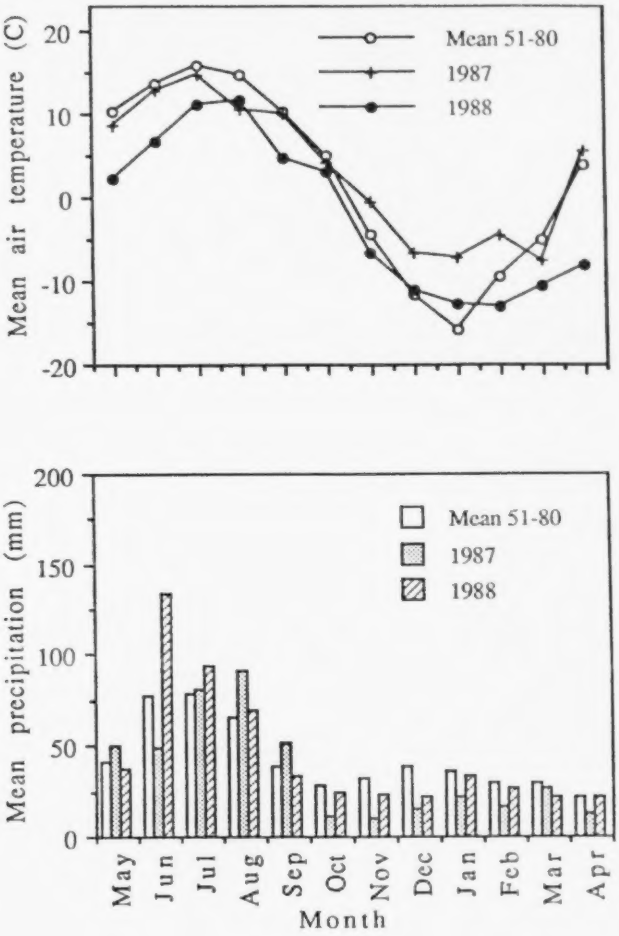


Figure 2.2: Monthly temperature and precipitation during 1987 and 1988 at the Goose River study area (G. Hillman 1989, unpublished data), and for 1951-1980 at Valleyview, central Alberta (Environment Canada n.d.).

Table 2.1: Means of selected soil properties of the experimental black spruce area at Goose River, central Alberta[a].

Soil depth	Bulk density	pH (H20)	Total C	Total N	Organic P	Exchangeable K^+
cm	$Mg.m^{-3}$		-----------	%	------------	$cmol(+)kg^{-1}$
5-0[b]	0.02	4.4	46.0	1.1	0.09	3.0
0-10	0.03	4.6	43.1	1.1	0.11	2.1
10-20	0.07	4.8	33.3	1.1	0.13	2.1
20-30	0.29	5.0	23.3	0.4	0.12	1.7
30-40	1.07	5.4	8.0	0.3	0.07	0.7
40-50	1.46	5.9	5.1	0.1	0.07	0.5
50-60	1.61	6.3	1.3	0.1	0.05	0.6

[a] Number of observations for bulk density ranged from 2 - 8, and for other properties from 3 - 4.

[b] Mostly live moss. Generally, the von Post humification varied between 2 and 4 to 40 cm depth.

2.2.2 Experimental design

The study area was drained in summer 1986 by excavating a network of drainage ditches with a backhoe in 135 ha, 42% of the total area of the peatland. Secondary ditches were 40 m apart and about 90 cm deep. The experiment was a split-split plot design replicated four times as randomized blocks (Alberta Forest Service 1987) with the following factors: main factor - stand density; subfactor - fertilization; and subsubfactor - distance from drainage ditch. These factors are described in Table 2.2. Nitrogen was applied as NH_4NO_3, P as triple superphosphate, and K as KCl; all compounds were agricultural grade.

Blocking at the time of plot establishment was based on peat thickness as observed in drainage ditches. Subsequent measurement within blocks gave mean peat thicknesses (cm) for the four blocks of 37(19% coefficient of variation), 40(25%), 43(26%), and 47(23%)

Table 2.2 Experimental factors at Goose River, central Alberta.

Factor	Description
Stand density	
Unthinned	Natural stand (control) 6580 stems.ha^{-1}
Thinned	ca 1610 stems.ha^{-1}
Fertilization	(kg.ha^{-1})
Unfertilized	Control
N	200
P	100
K	100
NP	Same individual doses as above
PK	
NK	
NPK	
Distance (m)	
Proximate	4 to 8
Distant	17 to 21

(Appendix 11.1). Each block was divided into two main plots, each 35 x 96 m. Within the main plot were eight contiguous fertilizer subplots each 12 x 35 m with the smaller dimension at a ditch edge. Rectangular subsubplots were 12 m in length, parallel to a drainage ditch.

The naturally-regenerated black spruce stand was manually thinned in March - April 1987 to a target mean density of 1,600 stems. ha^{-1} (ca 53% of stand basal area remained) with a tolerance of ±10% to give between 1,440 and 1,760 stems.ha^{-1} among main plots. Slash was left on the plots. Residual trees were selected as dominant or codominant (height criterion) with a symmetrical live crown and visually free of damage or disease. Additionally, a uniform spacing of acceptable trees was sought from what appeared to be a clumped distribution. Individual fertilizer materials were hand broadcast over each plot on 8 - 9 June 1987, when candles of black spruce were beginning to appear.

2.2.3 Soil sampling and profile description

2.2.3.1 Soil sampling

The soil was sampled from eight unfertilized subplots in late August and early September 1987 by one random organic/mineral soil core per subplot. Each core was divided into a 5 cm top (composed mainly of live moss) and thereafter 10 cm increments. Soil samples from the same depth increment in each block were bulked to make composite samples, which were stored at 2 - 5°C in sealed polyethylene bags.

2.2.3.2. Soil profile description and peat thickness measurement

Soil profiles were described in late August 1988. In order to ensure that the whole experimental area was somewhat represented, soil profile description was carried out at three different points. Profiles were described on a fresh cut on one side of a drainage ditch by noting horizon thicknesses, soil texture, color and roots. A sample from each horizon was collected into a polyethylene bag and transported to the laboratory for estimation of von Post degree of decomposition for organic horizons or particle size analysis of mineral soil. Soil profile descriptions are presented in Appendix 11.3.

Thickness of peat overlying mineral soil was measured by means of a graduated steel rod 1 cm in diameter and 1.5 m long in 50 per cent of the plots distributed uniformly over the study area. Within a plot, thickness was measured at six equally spaced points along a transect stretching from one ditch to the next along the middle line of each measured rectangular plot. The peat mineral soil boundary was detected by a sharp increase in resistance to penetration of the rod (Day *et al.* 1979). This method measured peat thickness to an accuracy of ± 15 cm. Mean peat thickness data within the experimental area are presented in Appendix 11.1

2.2.4 Sampling and pretreatment of foliage

Foliage was sampled during the fourth week of August 1988. At least four dominant and/or codominant black spruce trees were randomly selected for foliar sampling in each subsubplot; i.e., each distance class, excluding a 3 m buffer zone between subplots. Branches were sampled by means of a pruning pole from the upper one third of the crown excluding the first two or three whorls (Lowry and Avard 1965). Visually equal amounts of current and one-year-old needles were separately composited before subsampling and storage at 2 - 5° C. Mean weight was determined from two subsamples of 100 needles after 70°C drying and equilibration at room temperature and humidity. Needle subsamples were ground to pass a 100 mesh sieve for C, N, P and K analyses as described below.

2.2.5 Foliage and soil analysis

Mineral soil particle size distribution was determined by the hydrometer method as described by McKeague (1978). The degree of decomposition was estimated according to the von Post scale of humification as described by Landva *et. al.* (1986). One subsample of oven dry soil (70° C) was ground to pass a 10 mesh sieve for pH and exchangeable K analyses. A second soil subsample was ground to pass a 100 mesh sieve and digested for C, N, P and K analyses as described below. Soil pH was determined by means of a hydrogen electrode pH meter at distilled water:soil ratios of 2:1 (mineral samples) and 20:1 (organic samples). Total carbon was analysed by a Leco automatic analyser (Leco CR-12 Carbon Systems 981-600, LECO Corp., St. Joseph, MI). Exchangeable K extracted from duplicate samples of soil (McKeague 1978) and K in digests were determined by flame emission spectrophotometry (Perkin-Elmer Model 503, Perkin-Elmer Corp., Analytical Instruments, Norwalk, CT).

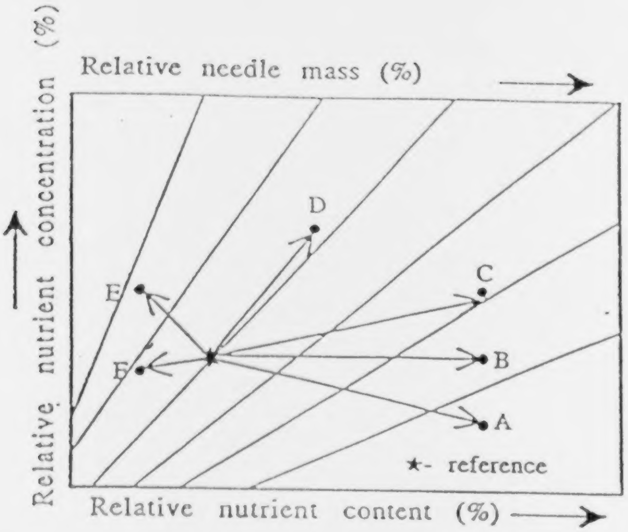
Soil and foliar subsamples were digested in concentrated sulfuric acid followed by oxidation with hydrogen peroxide (Lowther 1980), and total N and P in digests were determined by means of an auto analyser (Technicon Instruments 1977a,b). The mean deviations between my results and those of the National Institute of Standards and Technology No. 1575 pine needles reference sample were a relative +0.42% for N and -13% for P, using one reference sample per 16 foliar samples.

2.2.6 Data analysis

Statistical analyses of foliar responses were carried out on a mainframe computer using the UANOVA multivariate analysis of covariance programme developed at the University of Alberta (T. Taerum, pers. commun.). Homogeneity of variance was tested by the Bartlett-Box method (T. Taerum, pers. commun.) for each error term; virtually all variances were normally distributed. Moderate violations of assumptions of homogeneity are known to have little effect given the robustness of the F-ratio test (Winer 1971). The effects of stand density, fertilization and distance were analysed using a split-split plot design. The data were then sorted into either thinning or distance levels followed by planned contrasts for fertilization levels (Milliken and Johnson 1984) using SPSS-x (Norman 1983).

Further interpretation of foliar mass, N, P and K data was achieved by adopting the vector (diagnostic and predictive) analysis technique refined by Timmer and Stone (1978) and Timmer and Morrow (1984). The technique compares foliar mass, nutrient concentration and content to diagnose nutrient sufficiency, deficiency, luxury consumption, toxicity and antagonism, based on the magnitude and direction of the vector responses (Timmer and Stone 1978; Timmer and Morrow 1984; Timmer 1985; Fig. 2.3). The technique has additional advantages: a) simultaneous comparison of multiple nutrients in a single nomogram, b) identifies nutrient interactions, and c) effective where simultaneous excess and deficiency of several nutrients may be involved (Timmer 1985).

The sensitivity and reliability of this technique are greater when consideration is limited to the first year responses after treatment application, and to current foliage from tree species with a high degree of growth predetermination. Under these conditions measures of growth and nutrient uptake on an individual needle basis are not


Relative needle mass (%)
Relative nutrient concentration (%)
Relative nutrient content (%)
D
C
E
B
F
A
★- reference

	Change in relative				
Direction of shift	Needle mass	Nutrient concn.	Nutrient content	Physiological interpretation	Possible diagnosis
A	+	-	+	Dilution	Nonlimiting
B	+	0	+	Sufficiency	Nonlimiting
C	+	+	+	Deficiency	Limiting
D	0	+	+	Luxury consumption	Nontoxic
E	-	++	+	Excess	Toxic
F	-	-	-	Excess	Antagonistic

Figure 2.3: Interpretation of directional relationships among relative nutrient concentration, content, and mass of needles in response to treatment (adapted from Timmer and Stone (1978) and Timmer and Morrow (1984)).

confounded by treatment induced changes in needle number (Timmer and Morrow 1984; Timmer and Ray 1988).

In my study, foliar samples were taken during the second growing season after thinning and NPK fertilizer application. This may have compromised the sensitivity and reliability of the vector analysis technique due to confounding effects resulting from treatment induced increase in needle number. However, this approach is much better than the critical nutrient level approach whose applicability is constrained by the variability in genetic, climatic and stand conditions, and sampling and analysis protocols (Timmer and Morrow 1984). Furthermore, critical nutrient levels have not been determined for pole-sized black spruce.

2.3 RESULTS AND DISCUSSION

2.3.1 Soil morphological properties

Peat thickness ranges from 30 to 60 cm (Appendix 11.1). The mineral soil substratum ranges from silt loam and silty clay loam to clay texture (Appendix 11.2). Generally peat is composed of a 20 to 30 cm thick Of horizon underlain by a 10 to 30 cm thick Om horizon. Since this is a shallow-peated area, tree roots are likely to exploit underlying mineral soil to take up more nutrients. The information on morphological characteristics of my study area are presented in Appendix 11.3.

2.3.2 Foliar mass and NPK

The effect of blocking was significant only for foliar P concentration (P=0.020, Table 2.3). These results show that in general the experimental area was uniform with respect to foliar nutrients and needle mass responses and blocking was unnecessary in this case.

2.3.2.1 Foliar NPK concentration and content

The effects of stand density and of the interaction of stand

Table 2.3: Summary of ANOVA (P-values) of foliar mass and N, P and K concentrations and contents of current-year needles of black spruce at Goose River, central Alberta.

	N		P		K		Needle mass
	concn.	content	concn.	content	concn.	content	
Block[a,b]	0.56[c]	0.13	0.018	0.97	0.67	0.57	0.54
Den.	0.10	0.024	0.027	0.020	0.47	0.06	0.029
Fert.	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Den. x Fert.	0.32	0.065	0.070	0.009	0.054	0.43	0.037
Dis.	0.26	0.64	0.39	0.27	0.93	0.78	0.81
Den. x Dis.	0.098	0.21	0.024	0.24	0.57	0.86	0.56
Fert. x Dis.	0.059	0.005	0.009	<0.001	0.55	0.041	0.017
Den x Fert. Dis	0.36	0.62	<0.001	0.004	0.55	0.97	0.41

[a] Den. - stand density, Fert. - fertilization, Dis. - distance class from the edge of the drainage ditch.

[b] Degrees of freedom for block, Den., Error 1; Fert., Den. x Fert., Error 2; Dis., Den. x Dis., Fert. x Dis., Den. x Fert. x Dis. and Error 3 were 3, 1, 3, 7, 7, 42, 1, 1, 7, 7 and 48, respectively;

[c] Probability for a greater F-value.

density (thinning) with fertilization on N, P and K concentrations and contents of one-year-old (1987) needles were not significant (results not shown). The response patterns of foliar N, P and K concentrations and contents in one-year-old and current-year (1988) needles to fertilization treatments were in most cases similar. Thus only results for current needles are discussed. A further justification for use of current-year needles only was the fact that nutrient responses of this age class had a higher correlation with stemwood response than those of older needles of ***Pinus sylvestris*** (Leyton and Armson 1955) and ***Pinus pinaster*** (Keay *et al.* 1968), and contributed most to the photosynthetic capacity of the tree (***Pseudotsuga menziesii***, Brix 1971). However, Hom and Oechel (1983) found that current to four-year-old needles of black spruce showed similarly higher rates of photosynthesis than older needles. Current year's needles of black spruce displayed lowest overall between-tree variation in element content and were considered more reliable than older needles for estimating site quality (Lowry 1970). In my case, current needles usually had higher P and K concentrations and higher N, P and K content than one-year-old needles (P=0.001, paired t-test; data not shown).

Nitrogen

The mean foliar N concentrations of current needles from unthinned- and thinned-unfertilized plots were 0.86 and 0.96% respectively. Swan (1970) evaluated the seedling dry weight and foliar N concentration relationship of black spruce seedlings grown in sand cultures and concluded that the range of N concentration for moderate deficiency was 0.8-1.2%. Visual deficiency symptoms for black spruce seedlings grown in nutrient culture occurred between 0.6-1.0% foliar N (Swan 1960). The C/N ratio of the soil within 0-30 cm depth ranged from 30:1 to 58:1 (Table 2.1) suggesting that there was a high potential for microbial immobilization of N during decomposition of organic matter in unfertilized plots. According to Troth *et. al.* (1976) C/N ratios of 19:1-27:1 in forest floors of well-drained soils were indicative of favourable conditions for organic matter decomposition and rapid return of mineral N to soil organic layers. My foliar N concentration and soil C/N ratios suggest N was limiting the growth of black spruce.

Among main factors only fertilization affected foliar N concentration of current needles (P<0.001, Table 2.3). The foliar N concentration was not affected by stand density (P=0.10) or its interaction with either fertilization (P= 0.32) or distance from a ditch (P=0.098). However, the main effect of stand density (P=0.024), and its interaction with fertilization (P=0.065) on foliar N content (mass of element per unit needle) of current needles was significant (Table 2.3).

Addition of N along with P or K or both in unthinned plots resulted in longer vectors into the zone of deficiency than addition of these elements to thinned plots (Figs. 2.3 and 2.4a). These results suggest that N was more limiting to tree growth in unthinned than in thinned plots. Increased foliar N concentration and content in thinned-unfertilized (discussed below) plots may be related to the following: a) increased N availability due to reduced between-tree competition for N, b) enhanced mineralization of N as a result of higher soil temperature since more radiation was reaching the forest floor, c) improved ion mobility due to higher soil water content, and d) improved water relations leading to increased transpiration rates and higher water and ion uptake. Increased foliar N concentration and content in current needles may also be partly due to higher retranslocation of N from older needles in response to faster growth of current needles in thinned-unfertilized plots.

Addition of N alone in unthinned and thinned plots significantly increased foliar N concentration by 40 and 43% over unthinned- and thinned-unfertilized plots respectively (Fig. 2.4a). Addition of P or K or PK in unthinned and thinned plots did not increase foliar N concentration and content (Fig 2.4a). However, addition of N along with P or PK on unthinned plots significantly increased foliar N content more than addition of N alone (Fig. 2.4a, Appendix 11.5). In thinned plots, addition of NPK resulted in significantly higher foliar N content than N alone (Fig 2.4a, Appendix 10.6), probably due to a synergistic effect since N resulted in fast growth which in turn induced increased uptake of P and K.

Foliar N content was also significantly affected by a fertilization and distance interaction (P=0.0050, Table 2.3). Although foliar N concentrations and contents from unfertilized-proximate and -distant subsubplots were not significant (P=0.20, paired t-tests; Fig. 2.5 caption), foliar N concentration and content from unfertilized-proximate subsubplots were about 6 and 12% higher than those from unfertilized-

Figure 2.4: Effect of stand density and fertilization on relative unit needle mass and foliar concentrations and contents of nitrogen, phosphorus and potassium of black spruce. Mean foliar N, P and K concentrations of unthinned-unfertilized subplots were 0.86, 0.10 and 0.63% respectively, and of thinned-unfertilized subplots were 0.96, 0.13 and 0.73% respectively. Mean foliar N, P and K contents of unthinned-unfertilized subplots were 17.2, 2.09 and 12.7 ug needle^{-1} respectively, and thinned-unfertilized subplots were 22.3, 2.95 and 16.9 ug needle^{-1} respectively. Mean foliar mass of trees in unthinned- and thinned-unfertilized subplots were 2.01 and 2.32 mg needle^{-1} respectively. Star symbol represents the foliar statuses of unthinned- and thinned-unfertilized plots (reference) - equalized to 100. Vectors not shown in order to avoid overcrowding.

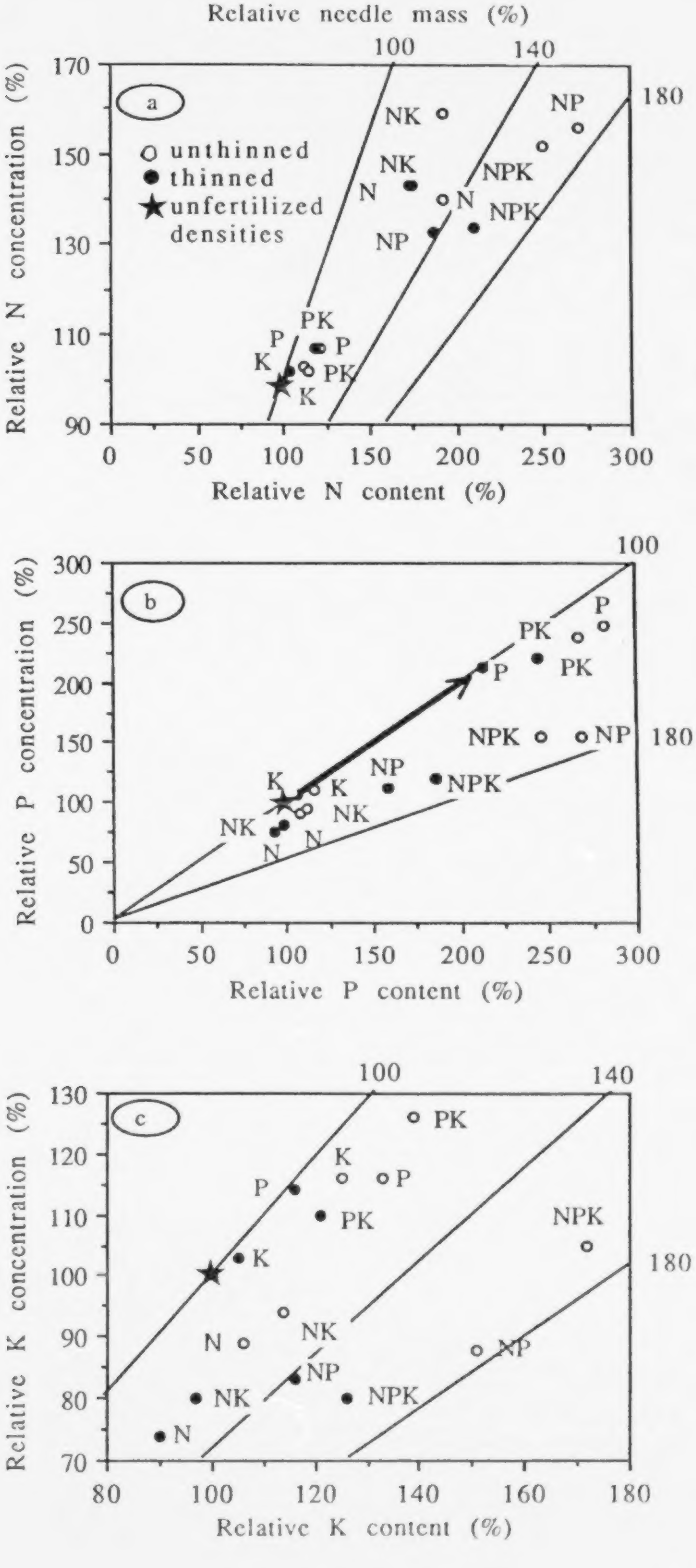
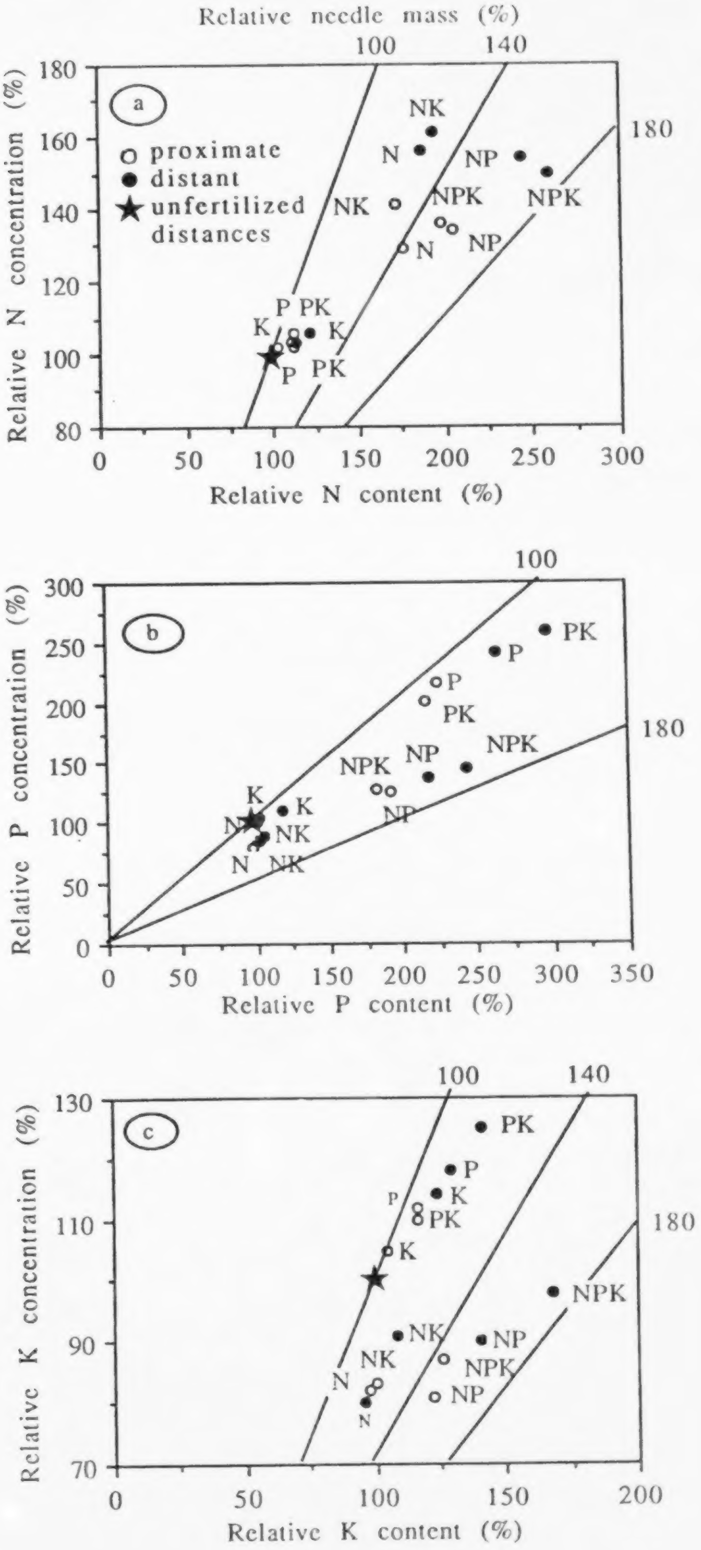

Relative needle mass (%)
100
140
180
a
unthinned
thinned
unfertilized densities
NK
NK
N
N
NP
NP
NPK
NPK
PK
P
P
K
PK
K
Relative N concentration (%)
170
150
130
110
90
0
50
100
150
200
250
300
Relative N content (%)
b
100
180
P
PK
PK
P
NPK
NP
NP
NPK
K
K
NK
NK
N
N
Relative P concentration (%)
300
250
200
150
100
50
0
Relative P content (%)
c
100
140
180
PK
K
P
P
PK
K
NPK
NK
N
NP
NP
NK
NPK
N
Relative K concentration (%)
130
120
110
100
90
80
70
80
100
120
140
160
180
Relative K content (%)

Figure 2.5: Effect of fertilization and distance from drainage ditch on relative foliar concentrations and contents of nitrogen, phosphorus and potassium of black spruce. Mean foliar N, P and K concentrations of unfertilized-proximate subsubplots were 0.94, 0.12 and 0.70% respectively, and unfertilized-distant subsubplots were 0.88, 0.11 and 0.66 respectively. Mean foliar N, P and K contents of unfertilized-proximate subsubplots were 20.9, 2.71 and 15.7 μg needle^{-1} respectively, and unfertilized-distant subsubplots were 18.7, 2.33 and 13.9 μg needle^{-1} respectively. Mean foliar mass of trees in unfertilized proximate and distant subsubplots were 2.23 and 2.10 mg needle^{-1} respectively. Star symbols represent the foliar status of unfertilized-proximate and -distant subsubplots (reference) - equalized to 100. Vectors not shown in order to avoid overcrowding.


Relative needle mass (%)
100
140
180
a
proximate
distant
unfertilized distances
NK
N
NP
NPK
NK
NPK
N
NP
P PK
K
K
P
PK
Relative N concentration (%)
180
160
140
120
100
80
0
50
100
150
200
250
300
Relative N content (%)
100
180
b
PK
P
P
PK
NPK
NP
NPK
NP
K
K
N
NK
N
NK
Relative P concentration (%)
300
250
200
150
100
50
0
0
50
100
150
200
250
300
350
Relative P content (%)
100
140
180
c
PK
P
K
P
PK
K
NK
NPK
NK
NP
N
NPK
NP
N
Relative K concentration (%)
130
110
90
70
0
50
100
150
200
Relative K content (%)

distant subsubplots. These trends may be attributable to both slightly higher availability and uptake of N due to an increase in N mineralization as a result of more favourable soil temperature, soil water and soil aeration in unfertilized-proximate subsubplots. The mean monthly depths to the water table at 5 m distance (proximate) from the ditch for the period of May through August in 1987 were 57, 47, 55 and 43 cm, respectively, and at 20 m distance (distant) were 35, 27, 33 and 25 cm, measured 0.5 km from my experimental area. For the same period in 1988 mean monthly depths to the water table at 5 m distance were 52, 42, 37 and 58 cm, and at 20 m distance were 33, 25, 26 and 37 cm, respectively (G.R. Hillman, unpublished data). Lieffers and Rothwell (1987a) noted from another Boreal peatland that in June and July the depth to the water table and daily mean soil temperature at 10 and 30 cm depths decreased with distance from the edge of the ditch. Hence, average soil gravimetric water content within the tree rooting zone of my recently drained peatland may be assumed to increase with distance from the ditch. Williams (1974) noted that N mineralization in organic soil was a minimum with the water table controlled at 18 cm depth and increased with water depth controlled at 34 cm. N mineralization rates of peat under laboratory incubation were higher under aerobic than anaerobic incubations (Isirimah and Keeney 1973).

However, N foliar responses from addition of N alone or with P or K were greater in distant than proximate subsubplots (Fig. 2.5a). This reversal in relative N foliar responses between the proximate and distant positions upon N fertilization suggests the influence of different limiting factors after fertilization. Perhaps reduction of N stress by fertilization magnified the effect of water availability controlling foliar responses in the proximate subsubplots. Rooting depth of black spruce in ditch profiles appeared to be limited to the thin surface organic stratum (ca 30 cm). As a consequence, water availability during the growing season could have been lower in the proximate position when the water table level was below the mean depth of the organic - mineral boundary. This boundary could effect a discontinuity in upward unsaturated flow. Also, the presumed higher water content in the upper soil horizons of the distant position would enhance diffusion rates of fertilizer ammonium and orthophosphate ions. In retrospect, needle water and soil water potentials for the distance treatments would allow the above hypothesis concerning black spruce water - N relations to be evaluated. Interactions among rooting, soil water availability and nutrient ion availability apparently affected foliar responses of black spruce.

As in the case of stand density, addition of NP and NPK in proximate and distant subsubplots resulted in significantly higher foliar N content than N alone (Fig. 2.5a, Appendix 11.5).

Phosphorus

The mean foliar P concentration for the unthinned- and thinned-unfertilized treatments were 0.10 and 0.13% respectively. The range of moderate P deficiency in black spruce seedlings grown in sand cultures ranged between 0.11 - 0.14% (Swan 1970). In my case, there may have been sufficient P for slow growth under conditions of N deficiency.

Significant responses in P concentration and content of current foliage occurred from the main effects of stand density and fertilization (Table 2.3). Thinning without fertilization significantly increased foliar P concentration by 30% over unthinned-unfertilized plots, i.e., 0.10 vs. 0.13% ($P<0.001$). These results may be attributable to similar reasons given above for foliar N response in thinned plots. Addition of P and PK in unthinned plots resulted in longer vectors into the zone of deficiency than addition of these fertilizers in thinned plots (Fig. 2.4b, Appendix 11.4). Similar trends resulted from NP and NPK additions. However, addition of P in unthinned and thinned plots resulted in significantly higher foliar P concentration than additions of NP or NPK (Fig. 2.4b, Appendix 11.6). This is because NP and NPK increased needle mass without concomitant increase in P concentration (dilution). On thinned plots, addition of P resulted in higher foliar P content than additions of NP and NPK (Fig. 2.4b, Appendix 11.6).

The interaction of stand density with distance on foliar P concentration was significant ($P=0.0235$, Table 2.3). Foliar P concentrations from unthinned-proximate and -distant, and thinned-proximate and -distant subsubplots were 0.10, 0.10, 0.14 and 0.12%

respectively. Thinning without fertilization increased foliar P concentration of proximate and distant subsubplots by 33 and 13% over unthinned-proximate and -distant subsubplots respectively. These results suggest that P was more limiting to tree growth in thinned-distant than in thinned-proximate subsubplots. Increased foliar P in thinned-proximate subsubplots may be related to higher rates of P mineralization and availability as discussed above for foliar N response to fertilization and distance.

The interaction of fertilization with distance from the ditch on foliar P concentration (P=0.009) and content (P=0.0001) was significant (Table 2.3). Addition of P alone, or with K on distant subsubplots resulted in longer vectors into the zone of deficiency than their addition on proximate subsubplots (Fig. 2.5b, Appendix 11.4). These results may be related to the complex interaction of P fertilizer and soil water as discussed above for N fertilizer. With the exception of foliar P content in distant subsubplots, addition of P alone in proximate subsubplots resulted in significantly higher foliar P concentration and content than the addition of NP and NPK (Fig. 2.5b, Appendix 11.6).

Potassium

Mean foliar K concentrations of 0.63 and 0.73% from unthinned- and thinned-unfertilized plots respectively were within the range (0.4 to 0.8%) of sufficiency for good to very good growth of black spruce seedlings (Swan 1970). Among the experimental factors only fertilization enhanced K concentration of current needles (P<0.0001, Table 2.3). Addition of P or K or both in unthinned plots resulted in longer vectors into the zone of deficiency than their addition on thinned plots (Fig. 2.4c, Appendix 11.4) suggesting lower availability of K in unthinned plots. On the other hand, any treatment with N gave vectors oriented into the zone of sufficiency or dilution (Fig. 2.4c, Appendix 11.4) indicating a non-stress condition for K.

Among fertilizer treatments accounting for the significant fertilizer by distance interaction upon foliar K content (P=0.041, Table 2.3), those with vectors in the deficiency zone (Fig. 2.5c) are of greater interest. For the P, K and PK treatments, the distant subsubplots had longer vectors than proximate ones, differences due more to K concentration than to needle mass. This response pattern is a tendency towards luxuary consumption of K. Within the two distances foliar K and mass responses were not significantly different for PK vs. P or K (Fig. 2.5c, Appendices 11.5 and 11.7)

2.3.2.2 Needle mass

The main effects of stand density and distance, and their interactions on mass of one-year-old needles were not significant (data not shown). Results presented hereafter are for mass of current needles, produced during the second growing season after thinning and fertilization. In general, current needles were significantly heavier than one-year-old needles ($P<0.05$, t-test, data not shown); overall unit needle masses were 2.6 and 2.3 mg needle^{-1} respectively.

The main effects of stand density ($P=0.0286$) and fertilization ($P<0.0001$) and their interaction ($P=0.0372$) on unit needle mass were significant (Table 2.3). Thinning without fertilization increased unit needle mass by 15% over unthinned-unfertilized plots, i.e., 2.01 vs. 2.32 mg needle^{-1}. This significant increase may be attributed to some increase in: a) soil N and P availability (higher foliar N and P concentration in thinned-unfertilized plots), and b) an unmeasured net assimilation rate due to reduction in shading of needles. In contrast, unit needle mass of black spruce growing on a well-drained Podzolic soil (2.7 mg needle^{-1}) did not increase during the second growing season following thinning (Weetman 1971).

However, the response in mass of needles of black spruce following thinning in my study was probably lower than what would have been obtained if trees were growing in well drained soil. This result may relate to the complex interactions of root-shoot ratio, photosynthetic product partitioning and soil N availability and uptake. The root-shoot ratio of peatland black spruce in early stages after drainage is presumably low (Kozlowski 1984). It has been hypothesized that in early stages after drainage the amount of photosynthate is probably low because leaf area (Dang and Lieffers 1989) and the root system (Lieffers and Rothwell 1987b) of black spruce are small. Thus, a higher proportion of photosynthate is probably allocated to the development of an extensive root system that is capable of supporting an expanding aboveground portion of the tree at a later stage of stand development and to crown expansion presumably by increasing the unit mass and number of needles. Ericsson (1981) showed that restricted N availability slowed canopy development, and resulted in an increase in proportion of carbohydrates that moved toward the roots of *Salix aquatica, S. fragilis and S. viminalis.* N-stressed *Pinus sylvestris* trees allocated more than 60% of their photosynthate belowground, whereas those receiving N supplements throughout each growing season allocated less than 40% of their carbohydrates to belowground (Linder and Axelsson 1982).

In unthinned plots, NP and NPK fertilizers gave 73 and 64% increment in unit needle mass respectively over unthinned-unfertilized plots, and in thinned plots, 41 and 55% respectively over thinned-unfertilized plots (Fig. 2.4). Addition of N alone in unthinned and thinned plots increased unit needle mass by 19 and 21% over unthinned- and thinned-unfertilized plots respectively (Fig. 2.2). Our modest foliar mass responses of black spruce to N fertilization alone are comparable to the responses obtained for 80-year-old black spruce growing on a 1.5 m deep peat in Minnesota (Alban and Watt 1981). Their needle mass increase due to N in unthinned plots ranged between 12 and 30%. They speculated that deficiencies in Mg and possibly some micronutrients may have limited N response.

Additions of P and PK in unthinned and thinned plots did not result in significant increases in unit needle mass (Fig. 2.4) suggesting that P availability did not limit needle production. At a higher dose (294 kg P ha^{-1}) foliar mass of current needles was 24% less than control (Alban and Watt 1981). Triple superphosphate at a high dose depressed the bole growth of naturally-regenerated peatland black spruce in Ontario, which was presumed to be a response to a decrease in soil pH (Payandeh 1982).

Although there was no main effect of distance on mass of current needles (P=0.806), interaction of distance with fertilization prevailed (P=0.0174, Table 2.3). NP and NPK on distant subsubplots increased unit needle mass by 59 and 73% over the unfertilized-distant subsubplot (Fig. 2.5a). In proximate subsubplots, NP and NPK gave increments of 52 and 46% (Fig. 2.5a). The larger response in needle mass in the distant position from NPK coincides with the relative difference in foliar N, but an interaction of NPK with soil water availability may contribute to the response also. Addition of NP and NPK resulted in significantly higher needle mass than addition of N alone on both proximate and distant subsubplots (Fig. 2.5, Appendix 11.5).

Addition of K alone or with P did not give a significant effect on needle mass. Similar results were obtained for black spruce elsewhere (Foster *et al.* 1986, Alban and Watt 1981). Thus, it appears that black spruce at the Goose River experimental area were not K-stressed.

2.4 CONCLUSIONS

a) Foliar N concentration of black spruce needles (current-year) produced during the second growing season after drainage indicated a suboptimum level of N in the natural (unthinned) and thinned 50- to 60-year-old, peatland stands. Foliar K and P concentrations were in a sufficiency range.

b) Trends in higher unit mass and higher N, P and K concentrations of current-year needles were responses to abrupt reduction in stand density from 6600 to 1600 stems ha^{-1}, probably as a result of increased N and P mineralization and ion mobility, and reduced shading and between-tree competition.

c) The N fertilization treatments significantly increased foliar N concentration and content of current needles over control. Concomitant increases in unit needle mass over control indicated that the drained, unthinned and thinned black spruce stands were N-limited. Foliar P contents following P and PK additions significantly increased, but unit needle masses did not change concomitantly.

d) Foliar N and P contents, and unit needle mass increased with distance from the drainage ditch under NPK addition, and for the last two response variables, under NP addition. This coincides with decreased depth to the water table and presumably increased water availability (this study area), and a lowering of the rooting-zone temperature (another study area, Lieffers and Rothwell 1987) with increased distance from the drainage ditches. I hypothesize my foliar responses are related to nutrient ion mobilities in soils of higher water table and to a diminished water stress of black spruce, if water stress occurs nearest to a ditch.

e) The previously documented delay of 3 - 6 years in radial increment response of black spruce to peatland drainage, which was attributed to preferential allocation of photosynthetic C to leaf and root tissues (Dang and Lieffers 1989), can likely be reduced by N and may be by P fertilization. My short-term foliar responses of black spruce to added N alone and in combination with P and K (single dosage of N though) suggest that the leaf area expansion rate (and presumably root also) triggered by a sudden lowering of water table can be accelerated through N fertilization to shorten the post-drainage lag in stemwood response.

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Chapter 3

FOLIAR RESPONSES OF TAMARACK AND BLACK SPRUCE TO DRAINAGE AND FERTILIZATION OF A MINEROTROPHIC PEATLAND

3.1 INTRODUCTION

In chapter 2, I reported the effect of thinning and fertilization of a shallow minerotrophic peatland on foliar responses of black spruce two years after installation of drainage ditches and during the second growing season after fertilizer application. In chapters 3 and 4 I examine how fertilization of contiguous undrained and drained minerotrophic peatland sites affects foliar responses of tamarack (*Larix laricina* (Du Roi) K. Koch) and black spruce (*Picea mariana* (Mill.) B.S.P.) two and three years after installation of drainage ditches at Wolf Creek, central Alberta. This peatland differs from the Goose River peatland in several aspects. The peat is thicker, trees are older and the stand density is much lower than that of the Goose River peatland site. The overstory species at Goose River was predominantly black spruce, whereas at Wolf Creek tamarack and black spruce are the overstory species.

In some drained peatlands in central Alberta, 3 to 6 years are required for the bolewood of black spruce to begin to respond to drainage (Dang and Lieffers 1989; Humphrey 1990). Dang and Lieffers (1989) postulated that immediately following ditching tree bole growth is low because of preferential allocation of photosynthate to root systems and leaf area. In chapter 2 I postulated that addition of N in the drained site could shorten the lag period for a significant initial response in tree bole growth. Supposedly, less photosynthate would need to be allocated to fine roots if the substrate is well supplied with mineral N (Brix and Mitchell 1980; Ericsson 1981; Linder and Axelsson

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1982; Axelsson and Axelsson 1986). Thus, more photosynthate may be available for development of needle mass and tree bole.

In a recently-drained and unfertilized peatland site, conifers may have stronger belowground sinks for photosynthate than those of a natural site because of their ability to increase root mass with depth due to improved soil conditions. On the natural site, the short-term strength of the belowground sink for carbon remains unchanged due to unaltered edaphic conditions. In this study, I hypothesized that peatland drainage without N fertilization would result in reduced leaf mass of conifers as compared to those growing in undrained-unfertilized soil. Furthermore, a larger foliar response to N addition would occur on the drained than on the natural site because of improved soil conditions.

This study was part of a larger project to evaluate the effects of drainage and fertilization of forested peatlands on ecosystem N, P and K dynamics and conifer growth responses. This chapter examines the effects of drainage (second and third growing seasons after ditching), NPK fertilization and distance from drainage ditch on needle mass, and foliar N, P and K concentrations and contents of tamarack and black spruce in the first and second growing seasons after fertilizer application. Chapter 4 presents elemental contents of soil organic fractions of peat 11 months following ditching, and foliar Ca, Mg and micronutrient status for tamarack and black spruce during the first and second growing seasons following fertilization.

3.2 MATERIALS AND METHODS

3.2.1 Study area

The minerotrophic peatland ("Wolf Creek", 53° 25.6'N lat., 116° 01'W long., Fig. 3.1) is within the Lower Boreal Cordilleran ecoregion (Corns and Annas 1986) and is classified as an intermediate fen based on water chemistry (Sjors 1952). Mean tree density among experimental

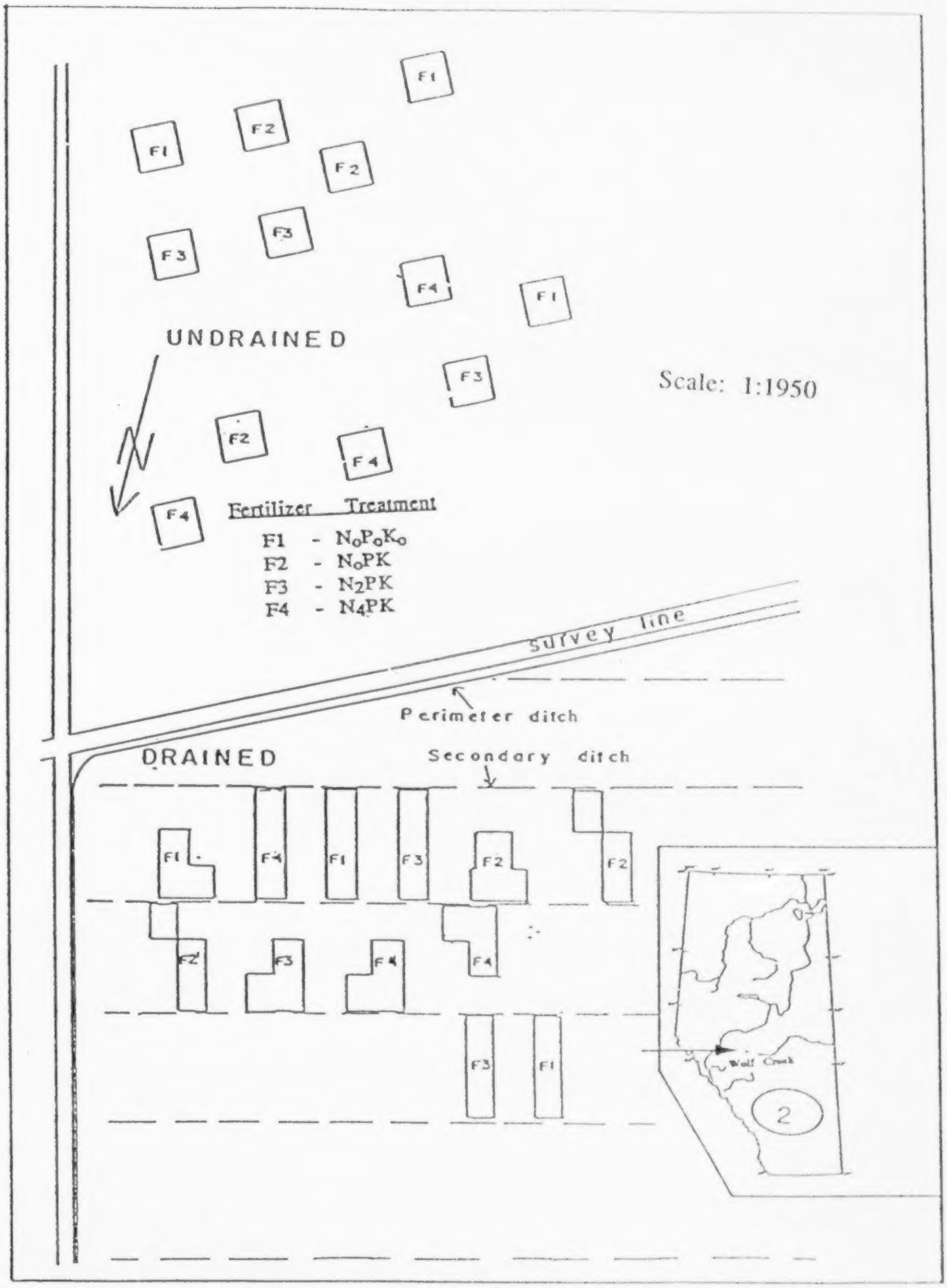

UNDRAINED
Scale: 1:1950
F1
F2
F3
F4
Fertilizer Treatment
F1 - $N_0P_0K_0$
F2 - N_0PK
F3 - N_2PK
F4 - N_4PK
survey line
Perimeter ditch
DRAINED
Secondary ditch
Wolf Creek
2

Figure 3.1: Location of the study area and layout of the experimental plots. Insert - map of Alberta. The site was ditched in fall 1987 and fertilized on 28 and 29 May 1989.

units in the natural tamarack/black spruce mixed stand ranged from 1740 to 2240 stems.ha^{-1} (basal area, 3.6 to 4.5 m^2.ha^{-1}) with tamarack accounting for over 85% of the stems. For tamarack (70 yr), on the undrained site mean dbh and height were 4.5 cm and 4.8 m, respectively, and on the drained site were 4.6 cm and 4.6 m, respectively. For black spruce (80 yr) on the undrained site corresponding values were 3.3 cm and 2.9 m, and on the drained site were 4.2 cm and 3.3 m. The understory consisted primarily of shrubs (*Betula pumila*, *Salix pedicellaris*, *Kalmia polifolia* and *Ledum groenlandicum*); herbs (*Carex* spp.), and mosses (*Sphagnum warnstorfii*, *S. angustifolium*, *Ptilium crista-castrensis*, *Tomenthypnum nitens*, *Pleurozium schreberi* and *Hylocomium splendens*).

The very poorly drained (unditched) Terric Mesic Fibrisol (Agriculture Canada Expert Committee on Soil Survey 1987) developed in 122 ± 10 cm (SD) of peat. The peat thickness on the drained site in September 1989 was 117 ± 12 cm (SD) (Appendix 11.8). The experimental area sloped approximately 1% towards the north. Selected soil properties for drained and undrained sites are presented in Table 3.1. The drained soil had slightly higher bulk density presumably due to subsidence of peat (Hillman *et al.* 1990). The pH in pedons sampled to 60 cm depth ranged between 5.4 and 6.1.

The region has a boreal, continental climate; mean annual air temperature and precipitation at Edson (924 m a.s.l.; 53° 35'N lat., 116° 25'W long., 35 km north-west) are 2.1°C and 572 mm, with 34% as snow. January and July air temperatures average -14.4 and 15.0°C. May through September precipitation totals about 398 mm (Envir. Can. n.d.). During the 1989 growing season (May - September) the mean monthly air temperatures at the study peatland were respectively 7.1, 12.2, 14.1, 12.4 and 8.2°C, and for May through August 1990 were respectively 6.6, 10.9, 12.5 and 13.0°C. The 1989 precipitation for May through September totalled 569 mm and for May through August 1990 was 398 mm (G. R. Hillman, unpublished data).

3.2.2 Experimental design

The experiment had three factors, ditch drainage (inferred

Table 3.1: Means of selected soil properties of undrained and drained sites before fertilization at Wolf Creek, central Alberta.

Site	Soil depth	Bulk[a] density	pH (H20)	Electrical conduct.	Total C	Total N	Organic P
	cm	$Mg.m^{-3}$		$dS.m^{-1}$	------------------	%	----------------------
Undrained							
	0-10	0.020 (0.001)	5.4	0.281	41.9 (0.29)	1.08 (0.034)	0.097 (0.004)
	10-20	0.044 (0.002)	6.1	0.166	40.4 (0.45)	1.44 (0.096)	0.125 (0.004)
	20-30	0.066 (0.003)	5.7	0.145	42.3 (0.25)	1.94 (0.080)	0.143 (0.004)
	30-40	0.096 (0.003)	5.5	0.095	44.0 (0.22)	2.56 (0.064)	0.127 (0.003)
	40-50	0.122 (0.003)	5.6	0.075	44.9 (0.25)	2.73 (0.039)	0.101 (0.002)
	50-60	nd[b]	5.6	0.071	45.5 (0.21)	2.69 (0.036)	0.089 (0.003)
Drained							
	0-10	0.019 (0.001)	5.4	0.311	42.2 (0.23)	1.03 (0.017)	0.093 (0.002)
	10-20	0.049 (0.002)	6.1	0.163	41.9 (0.23)	1.77 (0.058)	0.138 (0.005)
	20-30	0.086 (0.002)	5.7	0.118	43.1 (0.31)	2.55 (0.056)	0.144 (0.004)
	30-40	0.123 (0.002)	5.6	0.082	44.8 (0.20)	3.00 (0.050)	0.108 (0.003)
	40-50	0.139 (0.002)	5.6	0.070	45.4 (0.26)	2.88 (0.034)	0.089 (0.002)
	50-60	nd	5.6	0.069	45.3 (0.21)	2.88 (0.079)	0.084 (0.003)

[a] Numbers of observations (n) per depth increment for bulk density on undrained and drained sites were respectively 60 and 108; n=12 for other variables; standard errors are in parentheses.

[b] not determined.

differences in depth to water table), NPK fertilization, and distance from the edge of a drainage ditch at these levels:

i) Drainage: Undrained
Drained

ii) Fertilization:

	N	P	K
	----------	kg(kmol).ha^{-1}	-----------
Unfert.	0 (0.0)	0 (0.0)	0 (0.0)
N_0PK	0 (0.0)	80 (2.5)	120 (3.1)
N_2PK	200 (14.3)	80 (2.5)	120 (3.1)
N_4PK	400 (48.6)	80 (2.5)	120 (3.1)

iii) Distance : perpendicular distance from drainage ditch as two noncontiguous classes
Proximate - 4 to 8 m
Distant - 18 to 22 m

The undrained site was upslope about 75 m from the nearest drainage ditch of the drained site. Both sites were selected to minimize differences in stand density, understory species composition and tree size. The ditch network (Apppendix 10.9) was excavated with a backhoe (Lannen S-10 with a contoured bucket) in fall 1987 with parallel ditches 40 m apart and about 90 cm deep.

Twelve plots each 15 x 15 m and at least 10 m apart were randomly located in the undrained site. The twelve plots in the drained site were each 38 x 10 m with the smaller dimension at a ditch edge, and were spaced at least 5 m apart. Each drained plot was divided into two rectangular subplots 10 m in length parallel to a drainage ditch but different distances away from it. The four fertilization levels were randomly assigned to the twelve drained plots (each fertilizer level was replicated three times on each site). Fertilization levels were assigned to undrained plots such that control plots (unfertilized and N_0PK) were on an upslope position relative to the N dosage plots in order to minimize lateral contamination by N ions of control plots. Nitrogen was applied as urea $[(NH_2)_2CO]$, P as triple superphosphate and K as KCl. Dosages were selected on the basis of previous responses of black spruce to NPK fertilization in another peatland (see chapter 2). The mixed, agricultural-grade fertilizer materials were applied from a manually-operated cyclone seeder while making multiple perpendicular traverses in alternate directions on 28 and 29 May 1989. This was thirteen days on the undrained and nine days on the drained site after bud break in tamarack, and sixteen days on the undrained and twenty days on the drained site before bud break in black spruce.

3.2.3 Precipitation, soil and air temperature, and water table measurements

Precipitation, soil and air temperature, and water table on the undrained and drained sites were monitored by Dr. G. Hillman, Northern Forestry Centre, Edmonton, Alberta, Canada. Precipitation and air temperature were monitored at a meteorological station established at the study site. Groundwater configurations were monitored using 2 5-cm diameter wells installed on the undrained site and 9 similar wells on the drained site. Pressure transducers connected to LE8210-8K battery-driven data recorders, and Leupold-Stevens F-type water level recorders provided continuous records of the changes in water levels with time during the May through October period. Temperature probes were installed on undrained and drained sites. Each probe, connected to an LE8210-8K data recorder, supported sensors at 30 cm depth. Water table level and temperature data were recorded at 90-minute intervals. On the drained site, temperature and water table probes were installed at 20 m perpendicular distance from a drainage ditch.

3.2.4 Soil sampling and profile description

3.2.4.1 Soil sampling and analysis

The box sampler was used for taking soil samples. Five soil cores (8.1 x 8.1 cm horizontal cross-section) were randomly taken from each undrained plot and nine from each drained plot in July 1988. Each core was divided vertically into 10 cm increments to 60 cm depth. Soil samples were air dried and subsampled for estimation of air-dry water content before estimation of bulk density. Thereafter, soil samples taken from the same depth increment and same plot were composited, subsampled and stored at 0±3°C. One air-dry soil subsample was ground to pass a 20 mesh sieve for pH and electrical conductivity measurements. A second subsample was ground to pass a 100 mesh sieve for total N, organic P and K analyses following the digestion/quantification procedure specified in chapter 2.

3.2.4.2 Peat thickness measurement and soil profile description

Thickness of peat overlying mineral soil was measured as described in chapter 2. Within a drained plot peat thickness was measured at six equally spaced points along a transect stretching from one ditch to the next along the middle line of each measured rectangular plot. On the undrained site, peat thickness was measured at six randomly selected points. Mean peat thicknesses for undrained and drained sites are presented in Appendix 11.9.

Soil profiles were described in mid August 1991. Soil profile description was carried out at two randomly selected points on the undrained site and at three points on the drained site. Profiles were described on a freshly extracted soil core by noting horizon thicknesses, color and roots. Soil cores to 60 cm depth were extracted as described above. A sample from each horizon was collected into a polyethylene bag and transported to the laboratory for estimation of von Post degree of decomposition for organic horizons. Profile descriptions are presented in Appendix 11.10.

3.2.5 Foliar sampling and chemical analysis

At least three dominant and codominant trees per species per each of the 12 plots on the undrained site and per distance subplot on the drained site were selected and tagged in July 1988 for future foliar sampling. However, some plots or subplots had few or no acceptable black spruce trees based on relative crown position and apparent vigor. Foliage was sampled with a pruning pole on 31 August 1989 and on 2 September 1990 at the time of maximum foliar N and P concentration for tamarack based on 1989 biweekly sampling (see chapter 6). Maximum foliar N and P concentration for black spruce was reached in late September on the undrained site and in mid-October on the drained site.

Although Tyrrell and Boerner (1987) observed that foliar nutrient concentrations in tamarack did not vary with tree height, all tamarack branch samples were taken from the upper one-third of the crown. For tamarack, only short-shoots were sampled for unit needle mass and chemical analyses. Short-shoot, fascicular needles were not separated according to age of short-shoot stems since my preliminary data (not presented) indicated no age effect on foliar N and P concentrations. Visually-equal amounts of branches with short-shoot needles were composited and stored at -20°C in sealed polyethylene bags within 5 h after sampling. For black spruce, branch samples were taken from the upper one-third of the crown excluding the uppermost two or three whorls (Lowry and Avard 1965) and subsequently current and one-year-old needle subsamples were composited separately and stored as for tamarack.

Before the separation of short- and long-shoots of sampled tamarack branches as described above, the lengths of short-shoot needles and long-shoots were measured. Tamarack branches were composited per distance subplot only for the drained site and per plot for the undrained site. Thereafter, lengths of at least 20 long-shoots (lateral shoot elongation), and the maximum fascicular needle length of least 20 short-shoots on different aged portions of branches, were measured.

All foliar samples were dried at 65°C for 24 to 36 h and allowed to equilibrate at room temperature and humidity before needle separation. Mean weight was determined from four subsamples of 100 needles. Dry needles were ground to pass a 40 mesh sieve and then digested in sulfuric acid followed by oxidation with hydrogen peroxide (Lowther 1980). N and P were determined by auto analyser using industrial method No. 334-74/B+ (Technicon Instruments 1977) and K by flame emission spectrophotometer (Perkin-Elmer Model 503). The mean deviations of my results compared to those of the National Institute of Standards and Technology No. 1575 pine needle reference sample were a relative +0.21% for N; and - 0.13% for P using one reference per 15 foliar samples.

3.2.6 Data analysis

Only data of current needles for black spruce were analysed and are presented hereafter. Response patterns of foliar N, P and K concentration and content of current-year and one-year-old needles of black spruce to fertilization treatments of drained peatlands were similar (see chapter 2). Further justification from the literature for use of current needles was summarized in chapter 2.

Data for length of short-shoot needles and long-shoots, unit needle mass, and foliar N, P and K concentrations and contents were analysed on a mainframe computer using the UANOVA multivariate analysis of covariance programme developed at the University of Alberta (T. Taerum pers. commun.). Foliar N, P and K contents were calculated for each subplot (drained site) and plot (undrained site) as a product of unit needle mass and nutrient concentration. Data for each sampling date and for each species were sorted into two subsets for subsequent analyses: a) unfertilized and N_0PK, and b) N_0PK, N_2PK and N_4PK. Results for unfertilized plots were used as controls for testing the effects of N_0PK fertilization. For NPK fertilization, N_0PK was used as a control. The null hypothesis for homogeneity of error variance was tested by the Bartlett-Box method (T. Taerum pers. commun.) and not rejected.

The effects of distance and its interaction with fertilization on foliar mass, N, P and K concentrations and contents of tamarack and black spruce on the drained site in 1989 and 1990 were separately analysed for each species as a split-plot design (fertilization was a major factor and distance was a subfactor) and all were not significant ($P<0.05$), except foliar K concentration. Thus, these data from proximate and distant subplots were averaged. The analysis of variance (ANOVA) model tested for the effects of drainage, fertilization and their interaction. Following the ANOVA, significant responses were subjected to planned contrasts (Milliken and Johnson 1984) using SPSS-x (Norman 1983). In order to test the relationship between needle and long-shoot lengths of tamarack within each drainage level and each fertilization level, data were sorted by drainage and fertilization levels and each data subset was subjected to correlation analysis.

The vector analysis technique refined by Timmer and Stone (1978) was adopted for simultaneous comparison of foliar nutritional and growth responses. The technique compares foliar nutrient concentration and content, and mass to diagnose nutrient sufficiency, deficiency, luxury consumption, toxicity and antagonism, based on magnitude and direction of the vector responses exhibited by the three parameters in the nomogram (see section 2.2.6 and Fig. 2.3; Timmer 1985; Timmer and Morrow (1984); Timmer and Ray (1988)). In addition to employing the vector analysis during the second- and third-year after ditching, and second year after fertilization, the technique was also employed to diagnose responses of short-shoot needle of tamarack although it has an indeterminant growth of long-shoot needles. Long-shoots are sinks for nutrients and other cellular substances retranslocated from short-shoot needles. This could reduce mass and nutrient content of short-shoot needles. Retranslocation of cellular substances from current needles to other tree components of black spruce (determinant species) occurred during the summer (see chapter 6). This suggests that the vector analysis could also be applied to tamarack but results should be interpreted with caution.

3.3 RESULTS

3.3.1 Soil temperature and water table patterns

The drainage ditch network significantly (P=0.0001, paired t-test) lowered the water table (Fig. 3.2a,b) during May through September in 1989 and 1990. The mean water table depth on the undrained site was -22.4 ± 5.3 (SD) cm (1989) and -30.9 ± 7.6 cm (1990), higher than that of the drained site. Summer rainfall events resulted in higher water table levels with higher increases on the undrained site.

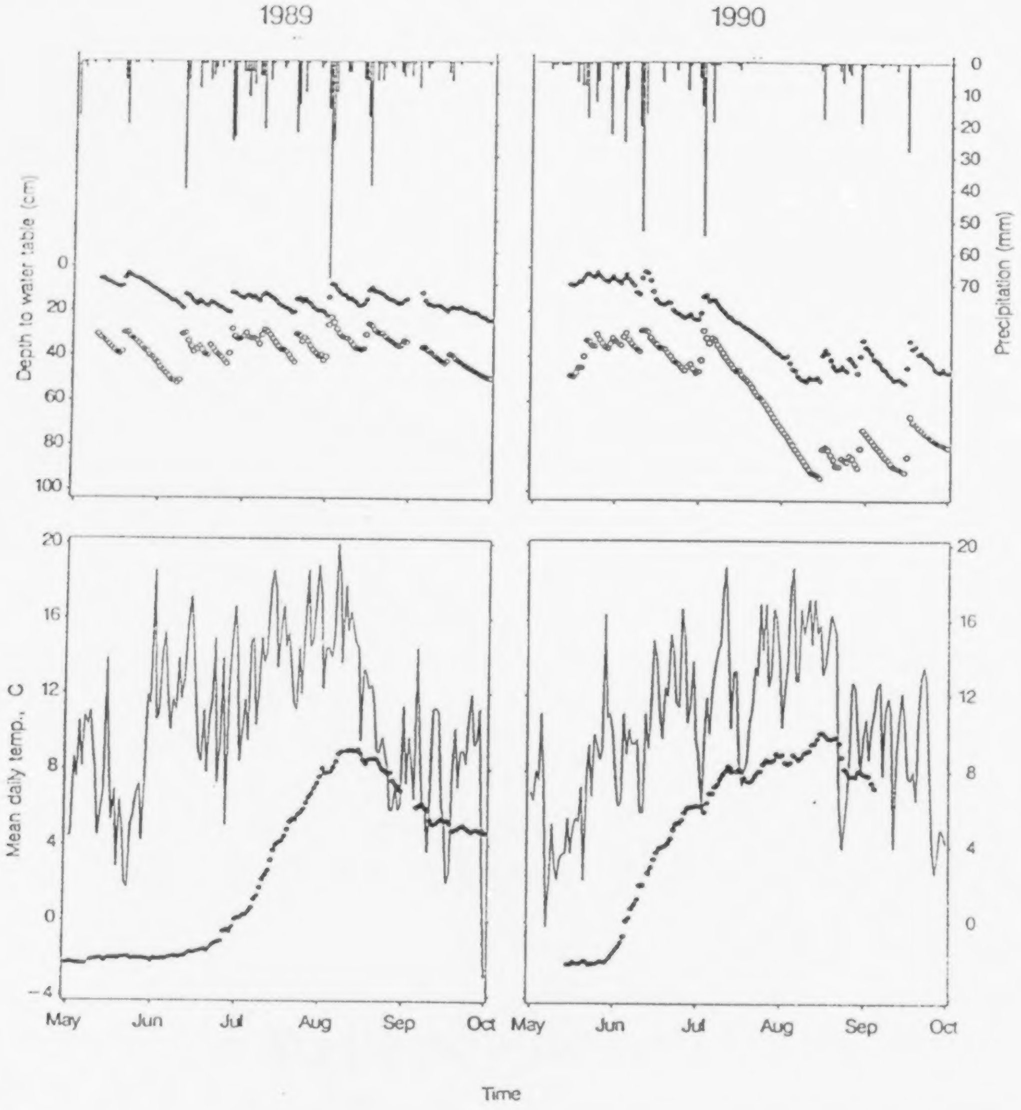


Figure 3.2: Daily mean depth to water table in undrained and drained sites and soil temperature in the undrained site (at 30 cm depth) (at 20 m perpendicular distance from drainage ditch) peatland sites, and daily precipitation and daily mean air temperature at Wolf Creek, central Alberta in 1989 and 1990. The undrained site is indicated by closed symbols and the drained site by open symbols. Hanging bars in graphs a) and b) indicate daily precipitation events. Continuous lines in graphs c) and d) indicate daily mean air temperature. (Source: Dr. G.R. Hillman, Northern Forestry Centre, Edmonton, Alberta, Canada, unpublished data).

Soil temperature patterns in relation to air temperature are given in Fig. 3.2c,d. Soil temperature data for the drained site was not taken because data loggers mulfunctioned in both years. However in 1989, monitering the recession of the upper frost boundary using an ice auger showed that the frost recessed faster and by mid June the frost had disappeared on the undrained site. To the contratry, the drained soil substrate the frost could be detected in early July. According to Lieffers and Rothwell (1986; 1987) undrained sites warmed up faster than drained sites in spring, but during the summer the mean soil temperature at 30 cm depth was on average higher relative to the undrained site.

3.3.2 Foliar NPK concentration and content

3.3.2.1 Nitrogen

Drainage significantly increased foliar N concentrations and contents of tamarack and black spruce in 1989 and 1990 ($P<0.05$, Table 3.2; Fig. 3.3), except N content of black spruce in 1989. For tamarack, the foliar N concentration increase due to drainage without fertilization was 77% in 1989 and 85% in 1990, while content increases varied from 66% to 150% (Table 3.3; Fig. 3.3a). For black spruce, drainage caused foliar N concentration increases of 23% in 1989 and 37% in 1990 (Fig. 3.3b). Foliar N concentration and content responses of tamarack to drainage were generally higher than those of black spruce (Fig. 3.3a,b).

N_0PK fertilization did not significantly affect foliar N concentrations and contents of tamarack and black spruce, and there was no significant drainage and fertilization interaction (Table 3.2; Fig. 3.4a,b). N fertilization and its interaction with drainage significantly ($P<0.05$) increased foliar N concentrations and contents of tamarack in both years (Table 3.4; Fig. 3.5a), except N content in 1989. For black spruce in both years, N fertilization significantly increased foliar N concentrations and contents (Table 3.4; Fig. 3.5b). Addition of either dosage of urea to the drained site resulted in luxury consumption of N by tamarack in 1989 (Fig. 3.5a). For tamarack in the undrained site in

Table 3.2: Summary of ANOVA (P-value) of foliar N, P and K concentrations and contents, unit needle mass of short-shoots of tamarack and of current-year needles of black spruce, and lengths of short-shoot needles (mm) and long-shoots (cm) of tamarack in response to drainage and N_0PK fertilization at Wolf Creek, central Alberta.

	N[1]		P		K		Needle mass	Length	
	concn.	cont.	concn.	cont.	concn.	cont.		Needle	Shoot
	1989 Tamarack								
Drain.[2]	0.001[3]	0.001	0.001	0.001	0.001	0.001	0.46	0.056	0.78
Fert.	0.17	0.56	0.001	0.001	0.001	0.001	0.005	0.40	0.82
D x F	0.14	0.59	0.001	0.001	0.002	0.002	0.080	0.35	0.89
	1989 Black spruce								
D	<0.001	0.38	<0.001	0.14	0.26	0.026	0.008	-	-
F	0.48	0.14	0.007	0.39	0.021	0.23	0.094	-	-
D x F	0.52	0.88	0.20	0.058	0.49	0.82	0.25	-	-
	1990 Tamarack								
D	<0.001	<0.001	0.002	0.001	0.002	0.004	0.006	0.003	<0.001
F	0.45	0.84	<0.001	0.001	0.006	0.13	0.93	0.15	0.97
D x F	0.55	0.69	0.002	0.035	0.11	0.45	0.67	0.97	0.51
	1990 Black spruce								
D	<0.001	0.033	<0.001	0.094	0.003	0.44	0.069	-	-
F	0.60	0.84	0.09	0.56	0.14	1.00	0.41	-	-
D x F	0.98	0.44	0.26	0.18	0.24	0.72	0.21	-	-

[1] N - foliar N; P - foliar P; K - foliar K; concn. - concentration (% dry wt. basis), cont. - content (ug nutrient needle^{-1});

[2] Drain - drainage, Fert - fertilization; Degrees of freedom for Drain, Fert, Drain*Fert and Error are 1, 1,1, and 8, respectively.

[3] Probability for a greater F-value.

Table 3.3: Effect of drainage and N_0PK fertilization on foliar N, P and K concentrations (% d.w. basis) and content (μg nutrient.needle^{-1}) and unit needle mass (mg.needle^{-1}) of tamarack and black spruce, and lengths of short-shoot needles (mm) and long-shoots (cm) of tamarack in 1989 and 1990, at Wolf Creek, central Alberta.

Response variable	Fertilization treatment	1989				1990			
		Tamarack		Black spruce		Tamarack		Black spruce	
		Undrained	Drained	Undrained	Drained	Undrained	Drained	Undrained	Drained
N conc.	Unfert.[a]	1.45[b]	2.55	0.92	1.13	1.52	2.63	0.77	1.05
	N_0PK	1.48	2.29	0.92	1.19	1.64	2.64	0.79	1.08
N content	Unfert.	6.38	10.4	29.9	32.9	7.25	16.8	26.9	30.8
	N_0PK	6.41	9.39	29.9	34.6	7.71	16.9	27.6	31.4
P conc.	Unfert.	0.22	0.39	0.15	0.19	0.28	0.34	0.13	0.16
	N_0PK	0.36	0.83	0.17	0.25	0.45	0.77	0.14	0.19
P content	Unfert.	0.99	1.62	4.88	5.53	1.34	2.18	4.54	4.69
	N_0PK	1.57	3.40	5.53	7.28	2.12	4.93	4.89	5.58
K conc.	Unfert.	0.64	0.85	0.63	0.71	0.69	0.83	0.57	0.69
	N_0PK	0.73	1.14	0.81	0.84	0.80	1.15	0.58	0.75
K content	Unfert.	2.82	3.42	20.9	24.7	3.29	5.31	19.9	20.1
	N_0PK	3.21	4.67	26.3	24.4	3.76	7.36	20.2	21.8
Needle mass	Unfert.	0.44	0.41	3.25	2.91	0.47	0.64	3.49	2.91
	N_0PK	0.43	0.49	2.94	2.79	0.50	0.70	3.12	3.01
Needle length	Unfert.	3.57	3.91	-	-	3.83	8.80	-	-
	N_0PK	3.86	3.98	-	-	4.38	8.30		
Shoot length	Unfert.	13.4	16.1	-	-	14.7	16.8	-	-
	N_0PK	15.0	16.0	-	-	14.9	18.0	-	-

[a] Unfert. - unfertilized plots.
[b] n = 3.

Table 3.4: Summary of ANOVA (P-value) of foliar N, P and K concentrations and content, and unit needle mass of short-shoots of tamarack and of current year needles of black spruce, and maximum lengths of short-shoot needles (mm) and long-shoot (cm) of tamarack in response to drainage and N_0PK, N_2PK and N_4PK fertilization at Wolf Creek, central Alberta.

	N[1]		P		K		Needle	Length	
	concn.	cont.	concn.	cont.	concn.	cont.	mass	Needle	Shoot
	1989 Tamarack								
Drain.[2]	-[4]	-	-	-	-	-	-	-	-
Fert.	0.001[3]	0.001	0.001	0.001	0.001	0.64	0.002	0.58	0.68
D x F	0.001	0.42	0.001	0.001	0.001	0.001	0.013	0.43	0.67
	1989 Black spruce								
D	-	-	-	-	-	-	-	-	-
F	<0.001	0.014	0.022	0.25	0.19	0.70	0.017	-	-
D x F	0.78	0.38	0.18	0.56	0.81	0.32	0.69	-	-
	1990 Tamarack								
D	-	-	-	-	-	-	-	-	-
F	<0.001	<0.001	<0.001	0.026	0.012	0.60	0.002	0.051	0.017
D x F	0.033	0.048	<0.001	0.073	0.14	0.67	0.77	0.59	0.17
	1990 Black spruce								
D	-	-	-	-	-	-	-	-	-
F	<0.001	0.081	0.16	0.62	0.90	0.64	0.92	-	-
D x F	0.20	0.40	0.15	0.82	0.90	0.29	0.18	-	-

[1],[3] As defined in Table 3.2;

[2] Drain - drainage, Fert - fertilization; Degrees of freedom for Drain, Fert, Drain*Fert and Error are 1, 2, 2, and 12, respectively;

[4] Not shown since it includes blanket application of N_0PK.

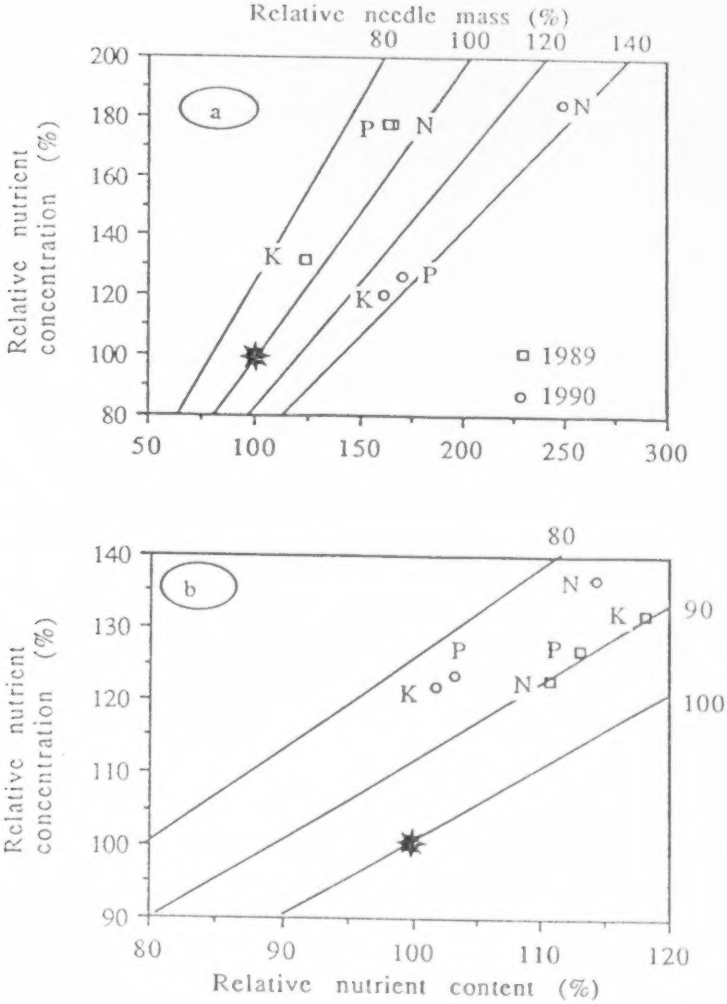


Figure 3.3: Effect of drainage on relative unit needle mass and foliar N, P and K concentrations and contents of (a) tamarack and (b) black spruce at Wolf Creek, central Alberta. Absolute mean unit needle mass, and foliar N, P and K concentrations and contents of tamarack and black spruce from undrained-unfertilized plots are given in Table 3.3. Star symbol represents foliar status of undrained-unfertilized plots (reference), equalized to 100; square symbols represent status for 1989 and circular symbols for 1990. Vectors not shown in order to avoid overcrowding.

Figure 3.4: Effect of drainage and NoPK fertilization on relative unit needle mass and foliar N, P and K concentrations and contents of tamarack and black spruce at Wolf Creek, central Alberta. Absolute mean unit needle mass, and foliar N, P and K concentrations and contents of tamarack and black spruce from undrained- and drained-unfertilized and -N_0PK plots are given in Table 3.3. Star symbol represents foliar status of undrained- or drained-unfertilized plots (reference), equalized to 100; solid symbols represent status for undrained-NoPK and open symbols for drained-NoPK plots. Vectors not shown in order to avoid overcrowding.

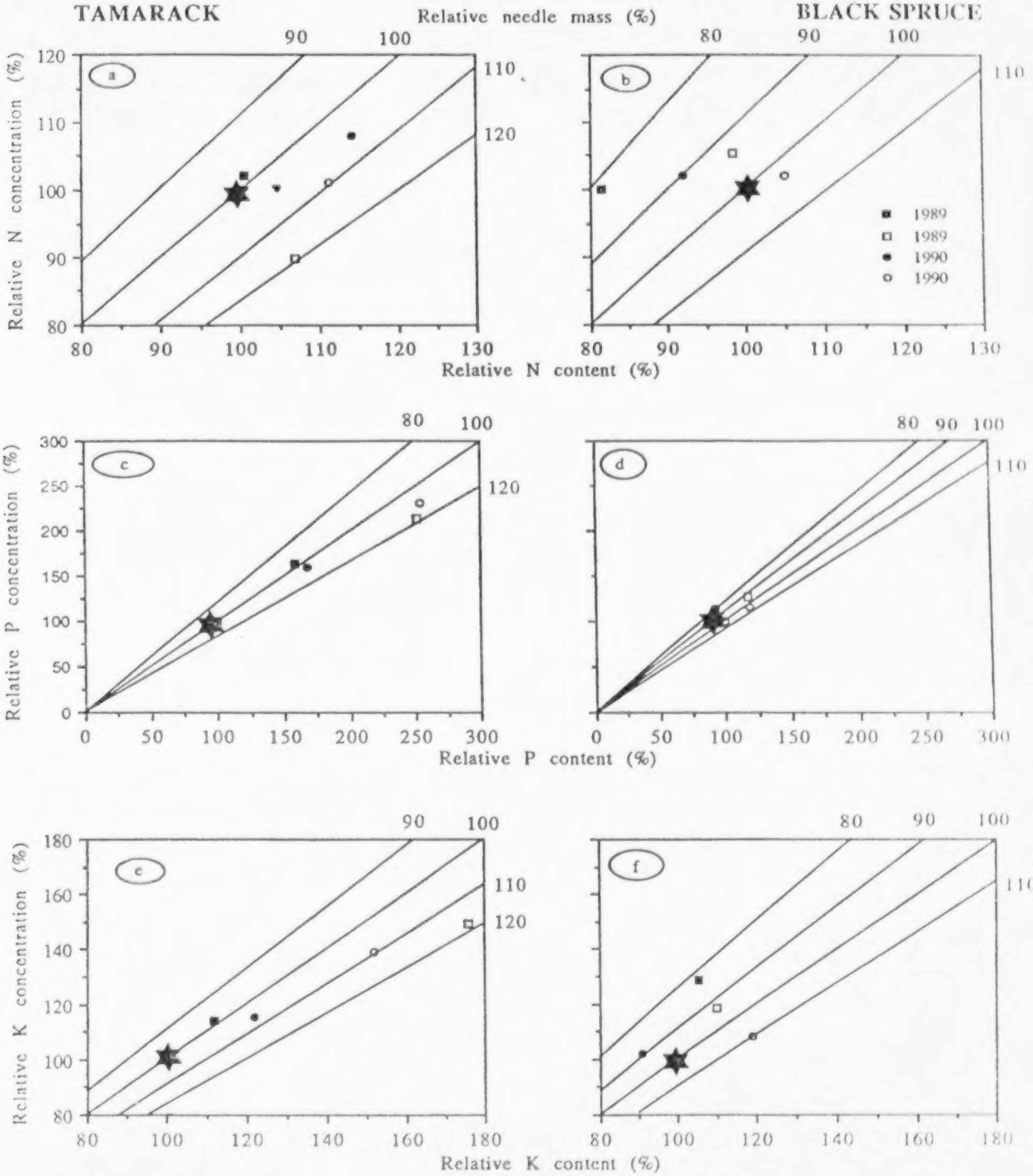
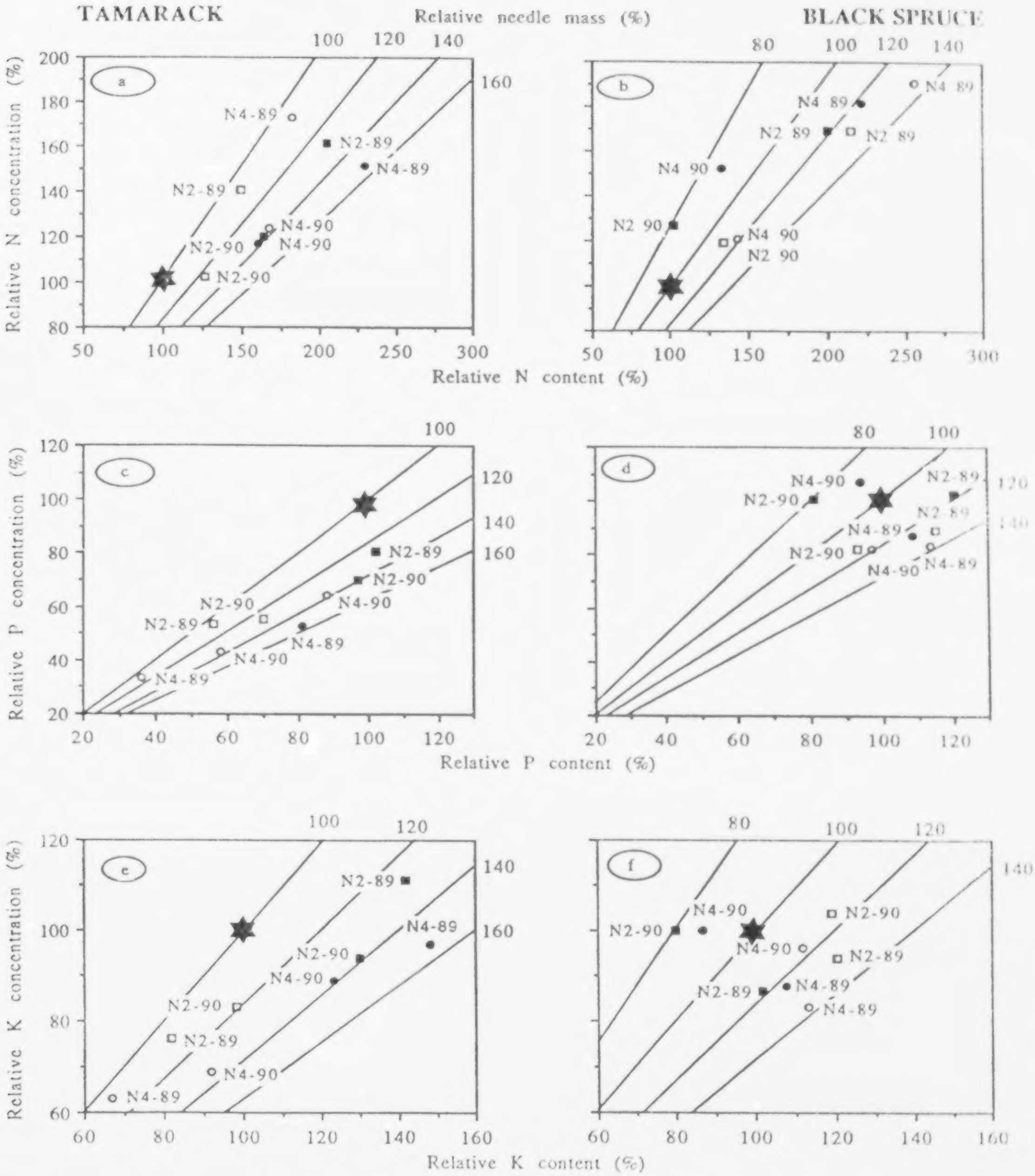

TAMARACK
Relative needle mass (%)
BLACK SPRUCE
a
b
c
d
e
f
Relative N concentration (%)
Relative N content (%)
Relative P concentration (%)
Relative P content (%)
Relative K concentration (%)
Relative K content (%)
■ 1989
□ 1989
● 1990
○ 1990
80
90
100
110
120

Figure 3.5: Effect of drainage and NPK fertilization on relative unit needle mass and foliar N, P and K concentrations and contents of tamarack and black spruce at Wolf Creek, central Alberta. Absolute mean needle mass, and foliar N, P and K concentrations and contents of tamarack and black spruce from undrained- and drained-N_0PK plots are given in Table 3.3. Star symbol represents foliar status of undrained- and drained-NoPK plots (reference), equalized to 100; solid symbols represent status for undrained-NoPK, and open symbols for drained-NoPK plots. Vectors not shown in order to avoid overcrowding.


TAMARACK
Relative needle mass (%)
BLACK SPRUCE
a
b
c
d
e
f
Relative N concentration (%)
Relative N content (%)
Relative P concentration (%)
Relative P content (%)
Relative K concentration (%)
Relative K content (%)
80
100
120
140
160
N4-89
N2-89
N4-90
N2-90
N4 89
N2 89
N4 90
N2 90

both years (Fig. 3.5a) and for black spruce in both sites in 1989 (Fig. 3.5b), N fertilization resulted in vectors suggesting that N was deficient. In sharp contrast, for black spruce in 1990, NPK on the undrained site resulted in excess foliar N that may have been toxic (Fig. 3.5b). Foliar N concentrations and contents of tamarack on the drained site were more responsive to N_4PK than N_2PK in both years (Fig. 3.5a; Appendix 11.11). On the undrained site in both years, foliar N concentration responses to N_4PK than N_2PK were not significantly different. In contrast, for black spruce only foliar N concentration in the undrained site in 1990 was more responsive to N_4PK than N_2PK (Fig. 3.5b, Appendix 11.12).

3.3.2.2 Phosphorus

Drainage increased foliar P concentrations and contents for tamarack and foliar P concentration for black spruce ($P<0.01$, Table 3.2; Fig. 3.3). Drainage without fertilization increased foliar P concentration of tamarack by about 77% (1989) and 28% (1990) over undrained-unfertilized plots, while content increase varied from 63% (1989) to 21% (1990) (Table 3.3, Fig. 3.3a). In contrast, for black spruce the corresponding increases in foliar P concentrations were respectively 13 (1989) and 24% (1990).

The effects of N_0PK (Table 3.2), N fertilization (Table 3.4) and their interactions with drainage on foliar P concentrations and contents of tamarack were significant ($P<0.05$) in both years. For P concentration in black spruce foliage, the main effect of N_0PK (Table 3.2) and N fertilization in 1989, and the interaction of N fertilization with drainage in 1990 were significant (Table 3.4). For tamarack in both years, addition of N_0PK in the drained site gave vectors oriented in a zone of dilution (Fig. 3.4c). On the undrained site, N_0PK resulted in luxury consumption of P (Fig. 3.4c), and the drained site was more responsive to N_0PK than the undrained site (Fig. 3.4c, Appendix 11.11).

Tamarack and black spruce on both sites responded differently, in terms of foliar P concentrations and contents, to N fertilization. For tamarack in both years, addition of NPK on both sites resulted in reduced foliar P concentrations and contents, although significantly much more on the drained site (Fig 3.5c, Appendix 11.11), demonstrating dilution. Addition of N on both sites in 1989, and on the drained site 1990, resulted in dilution of foliar P concentration of black spruce (Fig. 3.5d, Appendix 11.12). In 1990 on the undrained site, NPK resulted in excess foliar P concentration of black spruce that apparently was either toxic or antagonistic (Fig. 3.5d).

3.3.2.3 Potassium

Drainage increased foliar K concentration and content in tamarack for both years ($P<0.005$, Table 3.2; Fig. 3.3a). For black spruce, drainage increased foliar K content (1989) and foliar K concentration (1990) ($P<0.03$; Fig. 3.3b). N_0PK fertilization and its interaction with drainage significantly increased foliar K concentration and content of tamarack in 1989 ($P<0.003$, Table 3.2). For black spruce in 1989, N_0PK significantly increased foliar K concentration ($P<0.03$). Since vectors for foliar K were oriented in the zone of deficiency, the growth of tamarack in unfertilized plots may have been K-limited (Fig. 3.4e). Addition of N_0PK on the undrained site resulted in excess foliar K in black spruce that apparently was either toxic or antagonistic (Fig. 3.4f, Appendix 11.12).

Addition of NPK on the drained site in both years and on the undrained site in 1990 significantly ($P<0.02$, Table 3.4) reduced foliar K concentrations and contents of tamarack due to dilution since needle mass increased (Fig. 3.5e). In contrast, addition of NPK on undrained plots resulted in vectors oriented either into zones of deficiency or sufficiency in 1989 (Fig. 3.5e). N_4PK gave a greater reduction in foliar K concentration than N_2PK in 1989 (Fig. 3.5e, Appendix 11.11).

3.3.3 Needle mass

Drainage increased unit needle mass of tamarack by 36% in 1990 ($P<0.07$, Tables 3.2 and 3.3; Fig. 3.3), but decreased that of black spruce by 27 and 20% respectively in 1989 and 1990. The unit needle mass of tamarack was increased by NoPK in 1989 ($P<0.005$, Table 3.2), by N fertilization ($P<0.02$, Table 3.4) in both years and by the interaction of N fertilization with drainage ($P<0.001$) in 1989. The unit needle mass of black spruce was increased by N fertilization in 1989 only. In both years, tamarack needle mass was more responsive to N fertilization than black spruce. Increases in unit needle mass of tamarack on the undrained site due to N_4PK varied from 53% (1989) to 37% (1990) over NoPK plots and on the drained site varied from 7% (1989) to 33% (1990) (Fig. 3.5). That of black spruce ranged from 44% (1989) to 17% (1990) on the undrained site and from 5% (1989) to -12% (1990) on the drained site (Fig. 3.5).

3.3.4 Lengths of short-shoot needles and long-shoots

Drainage without fertilization significantly increased the maximum length of short-shoot needles by 10% (1989) and 130% (1990), and of long shoots by 14% (1990) over undrained-unfertilized plots (Tables 3.2 and 3.3). N_0PK produced no effect. The effects of urea fertilization on the maximum lengths of short-shoot needles and long shoots were significant in 1990 (Table 3.4). There was a 16% increase in mean length of needles and 24% increase in length of long-shoots due to addition of N_2PK on the undrained. Increases on the drained site were respectively 22 and 47% over drained-N_0PK plots (Table 3.3). On the undrained site maximum length of short-shoot needles was significantly positively correlated with length of long-shoots and unit needle mass, and on the drained site it was correlated with length of long-shoots in both years (Table 3.5). Length of long-shoots was correlated with unit needle mass on the undrained site in both years and on the drained site in 1990.

3.4 DISCUSSION

3.4.1 Effect of drainage

3.4.1.1 Foliar NPK

I am not aware of any study that evaluated foliar nutrient

Table 3.5: Pearson correlation coefficients describing the relationships among maximum needle length, long-shoot length and short-shoot unit needle mass for tamarack in undrained and drained sites at Wolf Creek, central Alberta.

	Undrained site			Drained site		
	nL[1]	sL	n m	n L	sL	n m
			1989			
n L	1	0.743*[2,3]	0.570*	1	0.718*	0.228
sL		1	0.754*		1	-0.038
n m			1			1
			1990			
n L	1	0.759*	0.648*	1	0.562*	0.113
sL		1	0.884*		1	0.652*
n m			1			1

[1] nL - maximum needle length, sL - long-shoot length, nm - unit needle mass. [2] Number of observations = 12.
[3] Significance indicated by * for $P \leq 0.05$.

concentrations for potential optimum productivity of semimature tamarack and black spruce. My measures of foliar N P and K concentration in unfertilized tamarack in undrained plots were within the range, and those in drained plots were high relative to those presented in the literature (Tilton 1977, 1978; Tyrrell and Boerner 1987). For black spruce, the foliar N of current-year needles in undrained- and drained-unfertilized plots was within the range for moderate deficiency in black spruce seedlings (Swan 1970). Foliar P concentration for tamarack in drained-unfertilized plots and foliar K concentration for black spruce in both sites were within the range of sufficiency for good to very good seedling growth (Swan 1970).

Drainage increased foliar N, P and K concentrations and contents of tamarack and black spruce during the second and third growing seasons after ditching. These results are consistent with those for tamarack and black spruce from a fen in central Alberta (Macdonald and Lieffers 1990) and for black spruce in the Great Clay Belt of Northern Ontario (Zdancewicz 1987). Increases in foliar N and P concentrations of current needles of the two species on the drained site may be attributable to reduced lateral movement of urea $NH4^+$ and orthophosphate ion, and to increased mineralization and uptake of N and P due to more favourable near-surface soil temperature, soil water and soil aeration. Lowering of water table may have increased N mineralization rates of peat (Williams 1974; Williams and Wheatley 1988; Isirimah and Keeney 1973).

My foliar N concentrations and soil C:N ratios suggest that N was limiting the growth of black spruce and that of tamarack on the undrained site. A similar conclusion was reached for black spruce in another drained, shallow peatland in north-central Alberta (see chapter 2). The C:N ratio of the soil within 0-30 cm depth in the undrained site ranged from 22:1 to 38:1 and in the drained site from 17:1 to 40:1 (Table 3.1), suggesting a potential for microbial immobilization of N during decomposition of organic matter. According to Troth *et al.* (1976), C/N ratios of 19:1 to 27:1 in forest floors of well drained soils are indicative of favourable conditions for organic matter decomposition and rapid return of mineral N to soil organic layers.

3.4.1.2 Needle mass and long-shoot length

Drainage decreased the unit needle mass of black spruce in unfertilized plots. These results are consistent with those of black spruce growing in drained-unfertilized peatland in the Clay belt of Ontario (J.K. Jeglum 1990 Pers. commun.). On the other hand, Zdancewicz (1987) observed that at the end of the first growing season following drainage needle mass of black spruce increased by 16% over undrained plots. My results may relate to interrelations of shoot/root ratio, photosynthetic product partitioning and soil N availability. The shoot/root ratio of peatland black spruce in early stages after drainage is presumably high (Kozlowski 1984). During early years after drainage, black spruce develops both root system and foliage as an acclimatization to the new environment. The restricted N supply indicated by foliar N concentration and decrease in needle mass on drained-unfertilized plots suggests that photosynthate might have been preferentially allocated to belowground than aboveground (Brix and Mitchell 1980; Ericsson 1981; Linder and Axelsson 1982; Axelsson and Axelsson 1986) in order to develop an extensive root system to take up more water and nutrients.

The comparison of net photosynthesis (see chapter 5) and unit needle mass of black spruce from unfertilized plots (this study) provides indirect evidence of the effect of drainage on the partitioning of photosynthate in black spruce, two and three years following ditch installation. Drainage increased net photosynthesis of black spruce from unfertilized plots in mid August 1989 and 1990 (see chapter 5). Assuming no change in photosynthate allocation pattern following drainage, then the unit needle mass of black spruce would be higher on the drained than on the undrained site. Since the opposite was true (Table 3.2; Fig. 3.3b), it is likely that a greater proportion of photosynthate was allocated to belowground on the drained than on the undrained site. As further indirect evidence, annual stemwood radial increments of black spruce were less than predrainage increments for three to six years following peatland drainage (Dang and Lieffers 1989).

For tamarack, drainage increased unit needle mass and length of long-shoots only during the third growing season (1990) after ditch installation. Interestingly, net photosynthesis of tamarack from the same plots did not significantly increase until 1990 (see chapter 5). Either tamarack had not acclimatized to the postdrainage soil environment for the first two years, or an uninvestigated limiting factor(s) existed, or a new equilibrium in photosynthate allocation pattern was reached within that period.

3.4.2 Effect of fertilization and its interaction with drainage

3.4.2.1 Foliar NPK

The lack of a significant effect of NoPK on foliar N concentration of tamarack and black spruce collaborates results of black spruce (Alban and Watt 1981; see chapter 2). Urea fertilization with PK increased foliar N concentrations and contents of tamarack and of black spruce in the drained site in both years, but on the undrained site urea resulted in excess foliar N apparently toxic to black spruce in 1990. The cause of this toxicity in undrained conditions is not known. Foliar N of drained black spruce near the end of the first growing season after fertilization with 336 kg $N.ha^{-1}$ as NH_4NO_3 was elevated by 50% over the 49 kg $P.ha^{-1}$ control (Alban and Watt 1981). My foliar N responses of pole-sized black spruce (undrained and drained) to urea fertilization support the foliar criterion for suboptimum N in black spruce seedlings (Swan 1970). Since unit needle mass of tamarack in undrained and drained plots was also increased by urea (discussed later), the growth of tamarack in unfertilized plots may also have been N limited.

The higher foliar N concentration of tamarack on unfertilized, undrained and drained sites versus that of black spruce (Table 3.3) suggests that tamarack has a higher potential to take up N, an observation similar to that of Small (1972), Tilton (1977), Tyrrell and Boerner (1987), Macdonald and Lieffers (1990) and Lieffers and Macdonald (1990). This could be mediated by different or more effective mycorrhizal fungi, since tamarack forms ectomycorrhizae with a genus-specific fungus, whereas black spruce forms ectomycorrhizae with a wide variety of fungi (Molina and Trappe 1982). Contrary to their hypothesis, my ^{15}N results (chapters 8 and 9) suggest that N uptake efficiency of tamarack is not as high as that of black spruce. High foliar N for tamarack may be related to high internal cycling since reabsorption of N from senescing needles is proportionately higher for tamarack than for black spruce (Small 1972; Tyrrell and Boerner 1987; see chapter 7).

Urea fertilization gave higher foliar P content of black spruce on drained plots in 1989 suggesting addition of N enhanced P uptake. However, N fertilization resulted in foliar P concentration of black spruce on the drained site that seemed to be toxic in 1990. Urea also decreased foliar P and K concentration and content in tamarack. Similar results were reported for several tree species (DeBell *et al.* 1975; Gill and Lavender 1983; Radwan and DeBell 1989; Munson and Timmer 1989).

There may be several reasons for reduced foliar nutrient concentration in the urea-PK plots. Increased needle mass due to N-fertilization likely diluted other foliar nutrients for tamarack on both sites (1989 and 1990) and for black spruce on both sites, except on the undrained site in 1990. For this exception, foliar nutrient dilution was not likely since urea decreased unit needle mass of black spruce. Alternatively, reduced uptake of N and P may have occurred. Radwan and DeBell (1989) speculated that reduced nutrient uptake following N-fertilization of *Tsuga heterophylla* may be related to: a) adverse effects of high NH_4^+-N concentrations on near-surface roots and associated mycorrhizae and b) the change in amounts or availability of some nutrients in the rooting zone effected by the direct or indirect action of the fertilizers and their transformation products. The toxic effects of ammoniacal-N on the undrained site cannot be ruled out, but such direct effects would be expected during the first growing season when $NH4^+$ concentration would be highest following urea hydrolysis. Toxic effects associated with ammoniacal-N are more evident near neutral pH for herbaceous plants grown in solution (Tolley-Henry and Raper 1986).

3.4.2.2 Needle mass

An increase in the unit needle mass of black spruce on both sites in 1989 due to urea fertilization is contrary to results reported elsewhere (Zdancewicz 1987; chapter 2). It was observed that at the end of the first growing season, 100 and 200 kg urea-N.ha^{-1} did not significantly affect mass of current-year needles of black spruce growing in drained peatlands. Brix (1981) and Brix and Ebell (1969) observed that needle mass increase of Douglas-fir in the first year of fertilization was negligible.

The lack of a significant effect from urea on the unit needle mass of tamarack in 1989 on the drained site suggests that growth of tamarack was either not limited by N availability or the trees had not acclimatized (discussed previously). Timing of urea application related to bud flush (two weeks after fertilization) was probably not the cause of this lack of response in needle mass since long-shoot length in 1989 was also not significantly increased. Because long-shoots have indeterminant growth, they can respond to N later in a growing season. Contrary to 1989 results, 1990 foliar mass of tamarack on both drained and undrained sites was increased by urea fertilization.

3.4.3 Needle phenology

Drainage and N fertilization have other indirect effects on the growth of tamarack and probably of black spruce. In addition to improved foliar nutrient status and increased foliar mass, drainage seemed to change timing of budbreak (refer to experimental design) and to prolong the photosynthetic period for tamarack. On the undrained site in 1989, needle senescence in tamarack as inferred from yellowing of needles started during the fourth week of August. By mid-September, all needles were yellow while those on the drained site showed little yellowing. By the end of September all needles of tamarack on the drained site had turned yellow. Seasonal foliar mass, and N, P and K content patterns of tamarack based on 1989 biweekly sampling (chapter 6) also provided indirect evidence of tamarack's earlier needle senescence on the undrained site. Foliar nutrients started to decline during the third week of August in unfertilized and N_0PK plots, and during the fourth week in urea plots on the undrained site versus early September in the drained site. On the undrained site, loss in needle mass began during the second and fourth week of August in non-urea and urea plots respectively.

3.4.4 Effect of distance

Essentially, there was no effect of distance and its interaction with NPK fertilization on foliar responses of tamarack and black spruce in this study, contrary to those of black spruce from the Goose River site, north central Alberta (see chapter 2). The Goose River site (minerotrophic peatland), had a shallow (30 to 60 cm) peat over silt loam and silty clay to clay soil of 1.6 $Mg.m^{-3}$ bulk density that appeared to restrict root growth and may have also restricted capillary rise since the mean water table level near the ditch for the period of May through August 1988 was below the mineral soil-peat interface. At Wolf Creek site, no significant differences in volumetric water content occurred in the 0 to 30 cm depth with perpendicular distance (near ditch, the quarter and the midpoint locations) from the 40 m ditch spacing in June through August 1989 (Rothwell and Silins 1990).

3.5 CONCLUSIONS

a) Distance from the drainage ditch had no effect on foliar mass or N and P concentration and content of tamarack and black spruce suggesting that the 40 m ditch spacing was probably appropriate.

b) Drainage significantly increased foliar N, P and K concentration and content of tamarack and black spruce probably as a result of increased mineralization and uptake due to more favourable soil temperature, soil water and soil aeration.

c) Drainage decreased the unit needle mass of unfertilized black spruce although its net assimilation rate was increased (chapter 5) relative to undrained-unfertilized plots, suggesting a greater proportion of photosynthate allocated to root development. In contrast, the unit needle mass of tamarack from unfertilized plots was increased by drainage, suggesting different acclimation mechanisms of the two species to drainage.

d) Addition of urea significantly increased foliar N concentrations and contents of tamarack and black spruce with a concomitant increase in foliar mass, except for black spruce in 1990. Thus, tamarack on undrained and drained sites was N limited. On the other hand, black spruce may have been N limited. Addition of PK alone increased foliar P concentration and content, and foliar mass of tamarack increased concomitantly indicating that P limited tamarack growth on the drained site.

c) My present results reinforce the hypothesis (chapter 2) that the previously documented delay of 3-6 years in stemwood radial increment response of black spruce to peatland drainage (Dang and Lieffers 1989) can be shortened through accelerated growth because of changing the photosynthate allocation pattern. Supposedly, a greater proportion of the photosynthate is allocated to aboveground instead of belowground components as a result of N addition to the drained site.

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Chapter 4

SOIL CHEMICAL PROPERTIES AND FOLIAR RESPONSES OF TAMARACK AND BLACK SPRUCE TO DRAINAGE AND FERTILIZATION OF A MINEROTROPHIC PEATLAND

4.1 INTRODUCTION

Peatland drainage may result in rapid changes in some soil physical properties such as increased bulk density (Rothwell and Silins 1990), soil aeration (Campbell 1980) and growing season soil temperature (Lieffers and Rothwell 1986, 1987). These changes may alter elemental content of organic soil due to increased rate of peat decomposition.

In the chapter 3 I examined the effect of ditch drainage and urea fertilization on needle mass and foliar N, P and K concentrations and contents for tamarack (*Larix laricina* (Du Roi) K. Koch.) and black spruce (*Picea mariana* (Mill.) B.S.P.). Drainage without fertilization increased foliar N, P and K concentrations and contents (mass of element per needle) for both species and unit needle mass for tamarack, but decreased mass of current needles of black spruce. These foliar changes may be related to improved soil conditions. Since urea fertilization resulted in concomitant increases in foliar N and unit needle mass, it appears that drainage alone did not alleviate suboptimal concentrations of foliar N that existed before ditching.

Nitrogen fertilization may disturb the normal balance of uptake of nutrients and may result in unpredictable patterns of change in concentration of various leaf nutrients (Waring and Schlesinger 1985; Paavilainen and Pietilainen 1983). Imbalance of macro- and micro-nutrient concentrations may cause growth disturbances (Paavilainen and Pietilainen 1983). The interaction effects of drainage and fertilization on essential tree nutrients in North American forested peatlands is undocumented, except for foliar N, P and K (chapter 3). In this chapter I examine: a) the effect of drainage on elemental concentrations of the peat; and b) the effect of drainage and fertilization on foliar calcium, magnesium and selected micro-nutrients.

4.2 MATERIALS AND METHODS

4.2.1. Study area, field and laboratory procedures

The peatland characteristics, experimental design, and soil and foliage sampling protocols are documented in detail in chapter 3 (section 3.2). The ditch network was excavated in fall 1987 and NPK fertilizers were applied on 28 and 29 May 1989. Foliage was sampled on 31 August 1989 and 2 September 1990. For peat, samples taken from 0 (surface of live moss) to 40 cm depth from unfertilized plots in July 1988 were analysed since tree roots were confined within this depth. Dry needles and peat were ground to pass a 40 mesh sieve and digestion was carried out by a modification of the dry ashing procedure (Ali *et al.* 1988). This procedure digests only the organic fraction of the soil. About 1 to 1.8 g oven-dry weight (70°C) of ground sample was dry ashed at 480°C for 16 to 24 h in a muffle furnace. For each plot on the drained site, a composite sample made up of equal amounts of foliar sample from each distance class (see chapter 3, section 3.2.2) was ashed. This is because the distance from the edge of drainage ditch had no effect on foliar responses of tamarack and black spruce at Wolf Creek (chapter 3, section 3.4.4). After cooling the ash was weighed and dissolved with 15 mL of aqua regia (HNO_3:HCl 1:4.5 volume ratio) and the solution heated to dryness. The dried residue was dissolved with 15 mL of 1.5 M HCl heated over medium heat for 15 min and the solution filtered through a Whatman No. 42 filter paper into a 50 mL volumetric flask. The filter paper and the crucibles were washed with warm deionized water into the flask. Filtered digests were analysed for Ca, Mg, K, Fe, Cu, Mn, Zn and B by inductively coupled plasma atomic emission spectrometry (ICP-AES) at the Alberta Agriculture Soils and Animal Nutrition Laboratory. Foliar and soil N and P were analysed as described in chapters 2 and 3. The mean deviations of my results compared to those of the National Institute of Standards and Technology No. 1571 orchard leaves reference samples were a relative percent of -20 (Fe), -5 (Cu), -11 (Mn), -15 (Zn), -

1 (B), -7 (Ca), and -9 (Mg) using one reference per 40 foliar or peat samples.

4.2.2 Data analysis

Soil nutrient and ash concentrations, and foliar nutrient concentrations and contents were analysed using the general linear models (GLM) procedure of SAS software (SAS Inst. Inc. 1987). For soil elemental concentrations, the ANOVA tested for the effects of drainage and soil depth. Prior to ANOVA, the null hypothesis for homogeneity of error variance was tested by the Shapiro-Wilk procedure (SAS Inst. Inc. 1987) and not rejected. The significant main treatments and/or their interactions were subjected to the LSD comparison procedure based on least square means (SAS Inst. Inc. 1987).

Foliar nutrient contents were calculated for each plot as a product of unit needle mass ($mg.needle^{-1}$) and nutrient concentration ($\mu g.g^{-1}$). For each plot on the drained site, mean unit needle mass of proximate and distant subplots was used since foliar samples from proximate and distant subplots were pooled for digestion. Then foliar data were sorted by sampling date and species, and each data subset was sorted into two groupings for subsequent analyses according to fertilizer levels: a) unfertilized and N_0PK, and b) N_0PK, N_2PK and N_4PK. Results for unfertilized plots were used as controls for testing the effects of N_0PK fertilization. For NPK fertilization, N_0PK was used as a control. The null hypothesis for homogeneity of error variance was tested as described above and not rejected. For foliar data, ANOVA tested for the effect of drainage, fertilization and their interaction on foliar nutrient concentrations and contents.

The vector analysis technique refined by Timmer and Stone (1978) was adopted for simultaneous comparison of foliar nutritional and growth responses (Appendix 11.4).

4.3 RESULTS AND DISCUSSION

4.3.1 Effect of drainage on soil elemental concentration

Drainage significantly increased total N, Mn and Zn concentrations, but decreased P concentration (ash free dry weight basis) of the peat (Tables 4.1 and 4.2). There were increased N, P Ca, Mn, Zn and Cu concentrations (v/v basis) in the 30 cm immediately below the lower limit of live green moss at least 10 years after lowering of the water table in central Alberta (Humphrey 1990). Increased ash, N and P contents of the 0-20 cm peat layer 27 years after installation of drainage ditches has been reported from a poor fen in Norway (Brekke 1987). For my study, increase in N and Zn concentrations may be related to negative enrichment (loss of carbon leaving behind other elements) related to peat decomposition. On the other hand, changes in Mn concentration may be attributable to both negative enrichment and its mobility in relation to redox potential as discussed above.

The effect of soil depth was significant (Table 4.1) for ash content and for concentrations of all elements of the peat. The following different patterns of change in elemental concentrations with depth were recognizable: a) ash, Mg, Fe, Mn, Zn and B reached maximum concentration between 10 - 30 cm and then decreased with depth, b) Ca, and Cu showed least concentration near the surface (0 - 10 cm) (Table 4.2).

These nutrient distribution patterns can be attributed to the following. The distribution of Fe and Mn is controlled by the redox potential of the peat. Under anaerobic conditions (low redox potential), Fe^{3+} and Mn^{4+} are reduced to divalent (Fe^{2+} and Mn^{2+}) states, and thus are changed from insoluble to mobile cations (Damman 1978). Thus it can be inferred that through mass flow and diffusion from the anaerobic zone they reach the oxidized soil-water interface where they are oxidized and precipitated in this zone of fluctuating water table level. B, Cu and Zn are probably not involved in oxidation-reduction reactions. But their mobility may be affected by some of the consequences of excess water (flooding). The reduction of the hydrous oxides of Fe^{3+} and Mn^{4+} and the production of organic complexing

Table 4.1: Summary of ANOVA (P-values) of elemental concentrations (ash free basis) and ash content of peat during the first growing season following installation of drainage ditches at Wolf Creek, central Alberta.

Response variable	Source of variation[a]		
	Drainage	Soil depth	D x S
Ash	0.36[b]	<0.001	0.99
N	0.002	<0.001	0.18
P	0.62	<0.001	0.12
K	0.14	<0.001	0.74
Ca	0.38	<0.001	0.96
Mg	0.63	<0.001	0.74
Fe	0.13	<0.001	0.59
Mn	0.053	<0.007	<0.001
Zn	0.048	<0.002	0.94
Cu	0.64	<0.001	0.16
B	0.085	0.011	0.34

[a] Degrees of freedom for Drainage, Soil depth, D x S and Error were 1, 3, 3 and 16 respectively;

[b] Probability for a greater F-value.

agents should increase solubility of Cu and Zn, and the formation of sulfides should lower their solubility. Elements mobilized in the reduced zone may diffuse upward and accumulate in the oxidized surface layers (Ponnamperuma 1972).

4.3.2 Foliar ash and nutrients

There has been no establishment of critical concentration of macro- and micro-nutrients in foliage of semi-mature tamarack and black spruce, but critical macronutrient concentrations exist for black

Table 4.2: Concentration of selected nutrients in peat during the first growing season following installation of drainage ditches at Wolf Creek, central Alberta.

Soil depth	Ash	K	Ca	Mg	Fe	Mn	Zn	Cu	B
cm	%	------------------		g.kg-1	------------------		-------	mg.kg-1	------
					Undrained site				
0-10	6.27a[2,3] (0.39)	3.15b (0.40)	12.6a (1.04)	2.18b (0.09)	2.20a (0.49)	7.21a (2.57)	127.3a (5.06)	1.52a (0.09)	12.7a (1.99)
10-20	11.2b (1.3)	0.81a (0.06)	20.7b (0.75)	2.41b (0.09)	22.2b (6.58)	18.1b (3.47)	196.8b (34.1)	2.63d (0.49)	25.9bc (3.04)
20-30	10.8b (0.96)	0.48a (0.03)	20.9b (0.61)	2.07b (0.12)	25.5b (3.72)	19.1b (1.71)	125.5a (12.8)	4.17c (0.38)	28.0bc (2.86)
30-40	9.46b (0.32)	0.61a (0.43)	19.7b (0.93)	1.62a (0.21)	12.8a (1.40)	5.42a (0.40)	84.9a (3.54)	3.70c (0.15)	20.1ac (0.34)
					Drained site				
0-10	5.87a (0.48)	2.82c (0.16)	12.8a (1.14)	2.17b (0.09)	1.33a (0.40)	4.19a (1.08)	102.1a (15.1)	1.39a (0.08)	11.4a (2.67)
10-20	10.8b (0.16)	0.66b (0.02)	21.8b (0.10)	2.42b (0.07)	20.7b (5.30)	26.9b (2.98)	164.5b (13.7)	3.26b (0.10)	22.2bc (0.93)
20-30	10.1b (0.36)	0.30b (0.02)	21.1b (0.62)	1.90a (0.08)	15.0bc (2.35)	3.75a (0.62)	91.6a (4.93)	3.50b (0.15)	16.8ac (1.71)
30-40	9.17b (0.52)	0.15a (0.01)	20.6b (0.89)	1.61a (0.07)	7.91ac (1.00)	1.61a (0.09)	70.7a (3.95)	3.40b (0.11)	19.3ac (5.69)

[1] Nitrogen and phosphorus concentrations are given in Table 3.1 (chapter 3);

[2] Number of observations per depth increment on each site was 3; standard errors are in parentheses;

[3] Within each site, means followed by the same letter within the same column are not significantly different ($P<0.05$).

spruce seedlings (Swan 1970). For tamarack in undrained- and drained-unfertilized sites, foliar Ca and Fe concentrations were lower than, but Mg and Zn were within the range reported from undrained peatlands by Tilton (1977, 1978), Wali and Bares (1979) and Tyrrell and Boerner (1987).

For black spruce, foliar Ca, Mg, Fe and Zn concentrations were lower than those reported from an alkaline peatland in Minnesota (Wali and Bares 1979), except for Mg in the drained site. Foliar Ca, Mg, Mn and Fe concentrations in tamarack and black spruce in unfertilized plots (Table 4.3) were higher than or within the range of those reported from undrained and drained peatlands in central Alberta (Lieffers and Macdonald 1990).

In general, average concentrations of foliar N, P (chapters 3 and 5), ash and other foliar nutrients, except Zn and Cu for tamarack in undrained- and drained-unfertilized plots were higher than those of black spruce (Table 4.3). However, foliar nutrient contents (mass of element per unit needle) in tamarack were lower than in black spruce. This is related to the lower unit needle mass of tamarack compared to that of black spruce (chapter 3). Higher foliar N and lower Ca concentrations in tamarack than in black spruce have been reported previously (Tyrrell and Boerner 1987; Lieffers and Macdonald 1990).

4.3.2.1 Drainage

Drainage significantly (P<0.001; Tables 4.4; Fig. 4.1) increased foliar ash concentration (dry weight basis) of both species in 1989 and 1990, with greater increase in tamarack. This result may be explained partly by increased foliar elemental concentrations as a result of drainage.

Species-specific responses to drainage (without fertilization) were evident in foliar nutrient status. The effect of drainage was significant for concentrations and contents of all foliar nutrients in tamarack, except for Mg concentration in 1989 and 1990, and for Ca contents in 1990 (Tables 4.3 and 4.4). Drainage resulted in luxury consumption (see Appendix 11.4 for definition) of all nutrients for tamarack in 1989 (Fig. 4.2a). The magnitude of luxury consumption

Table 4.3: Effect of drainage and N_0PK fertilization on foliar macro- and micro-nutrients concentration and content[1] of short-shoot needles of tamarack and and current needles of black spruce in 1989 and 1990 at Wolf Creek, central Alberta.

Response variable	Fertilization treatment	Tamarack				Black spruce			
		1989		1990		1989		1990	
		Undrained	Drained	Undrained	Drained	Undrained	Drained	Undrained	Drained
Ca concn.	Unfert.	3.77	6.03	3.96	6.09	2.46	3.52	3.22	3.47
	N_0PK	3.90	5.61	4.72	6.29	2.75	3.35	3.19	3.80
Ca content	Unfert.	1.66	2.50	1.90	4.20	9.26	11.2	11.0	10.0
	N_0PK	1.70	2.74	2.40	1.90	11.7	10.7	11.0	11.0
Mg concn.	Unfert.	1.36	1.77	1.80	1.87	0.72	1.15	0.82	1.19
	N_0PK	1.33	1.56	1.93	1.58	0.77	1.14	0.76	1.14
Mg content	Unfert.	0.59	0.73	0.86	1.26	2.82	3.32	0.28	0.34
	N_0PK	0.57	0.76	0.97	1.06	2.56	3.12	0.25	0.34
Fe concn.	Unfert.	57.2	138	64.4	94.0	41.3	41.6	27.0	20.6
	N_0PK	58.9	106	76.8	98.7	48.9	64.2	19.2	22.5
Fe content	Unfert.	0.025	0.057	0.031	0.064	0.17	0.12	0.0094	0.0059
	N_0PK	0.026	0.052	0.039	0.065	0.16	0.18	0.0062	0.0068
Mn concn.	Unfert.	621	1523	834	2308	614	734	684	696
	N_0PK	691	968	1016	1212	736	671	742	629
Mn content	Unfert.	0.28	0.63	0.40	1.56	2.49	2.15	0.24	0.20
	N_0PK	0.30	0.48	0.51	0.81	2.51	1.84	0.24	0.19

[1] Nutrient concentrations are in $mg.kg^{-1}$, except for Ca and Mg concentrations in $g.kg^{-1}$; all nutrient contents are in $\mu g.needle^{-1}$.

Foliar N and P concentrations and contents are presented in Table 3.3.

Table 4.3: continued.

Response variable	Fertilization treatment	Tamarack				Black spruce			
		1989		1990		1989		1990	
		Undrained	Drained	Undrained	Drained	Undrained	Drained	Undrained	Drained
Zn concn.	Unfert.	18.2	43.0	23.0	47.4	31.9	45.8	39.4	50.4
	N_0PK	21.5	35.4	26.0	47.4	32.1	49.2	30.3	55.9
Zn content	Unfert.	0.0080	0.018	0.011	0.032	0.13	0.13	0.014	0.015
	N_0PK	0.0093	0.017	0.013	0.032	0.11	0.13	0.010	0.17
Cu concn.	Unfert.	0.59	1.66	0.77	2.52	0.70	3.89	0.57	0.89
	N_0PK	0.67	1.51	1.52	2.93	1.76	2.65	0.60	2.19
Cu content	Unfert.	0.00026	0.00069	0.00037	0.0016	0.0027	0.012	0.00018	0.00025
	N_0PK	0.00028	0.00074	0.00075	0.0018	0.0061	0.0072	0.00014	0.00065
B concn.	Unfert.	49.3	55.3	31.3	36.9	18.9	22.9	17.9	19.1
	N_0PK	43.2	51.5	33.3	44.5	12.5	25.9	26.6	20.8
B content	Unfert.	0.022	0.023	0.015	0.025	0.072	0.069	0.00063	0.0055
	N_0PK	0.019	0.025	0.017	0.030	0.049	0.073	0.087	0.0062

Table 4.4: Probability values from ANOVA of foliar nutrient concentration[1] (c) and content[2] (ct) of tamarack and black spruce in response to drainage and NoPK fertilization at Wolf Creek, central Alberta.

Resp. var.[3]	Tamarack						Black spruce					
	1989			1990			1989			1990		
	D[4]	F	D x F	D	F	D x F	D	F	D x F	D	F	D x F
Ash	<0.001[5]	0.002	0.01	<0.001	<0.001	0.23	0.001	0.007	0.365	0.004	0.74	0.23
Ca c	<0.001	0.61	0.37	<0.001	0.10	0.31	0.042	0.16	0.18	0.18	0.62	0.57
Ca ct	<0.001	0.35	0.45	0.079	0.49	0.54	0.78	0.57	0.59	0.94	0.63	0.36
Mg c	0.087	0.22	0.25	0.25	0.77	0.58	<0.001	0.71	0.71	0.004	0.59	1.00
Mg ct	0.065	0.38	0.46	0.038	0.67	0.14	0.17	0.53	0.93	0.057	0.63	0.73
Fe c	0.014	0.48	0.44	0.01	0.33	0.65	0.44	0.16	0.46	0.70	0.47	0.24
Fe ct	0.009	0.77	0.71	0.001	0.44	0.59	0.70	0.52	0.35	0.30	0.41	0.18
Mn c	0.011	0.22	0.12	0.063	0.81	0.31	0.97	0.69	0.34	0.57	0.96	0.48
Mn ct	0.020	0.51	0.39	0.033	0.86	0.80	0.33	0.58	0.56	0.18	0.84	0.93
Zn c	<0.001	0.52	0.13	0.001	0.58	0.59	0.002	0.60	0.65	<0.001	0.58	0.050
Zn ct	<0.001	0.77	0.52	<0.001	0.77	0.58	0.29	0.54	0.47	0.024	0.53	0.064
Cu c	<0.001	0.71	0.25	0.019	0.30	0.75	0.11	0.94	0.33	0.33	0.58	0.25
Cu ct	<0.001	0.47	0.79	0.002	0.19	0.89	0.20	0.90	0.31	0.42	0.62	0.20
B c	0.026	0.093	0.67	0.004	0.049	0.21	0.83	0.39	0.32	0.010	<0.001	0.002
B ct	0.055	0.21	0.056	0.003	0.94	0.94	0.40	0.39	0.52	0.090	0.57	0.67

[1] concentration (% dry wt.);

[2] content (ug element.needle^{-1});

[3] Resp. var. - response variable;

[4] D - drainage, F - fertilization; Degrees of freedom were: Drainage = 1, fertilization = 1, D x F = 1 and error = 8;

[5] P>F-ratio.

Table 4.5: Probability values from ANOVA of foliar nutrient concentration[1] (c) and content[2] (ct) of tamarack and black spruce in response to drainage and N_oPK, N_2PK and N_4PK fertilization at Wolf Creek, central Alberta.

Resp. var.[3]	Tamarack						Black spruce					
	1989			1990			1989			1990		
	D[4]	F	D x F	D	F	D x F	D	F	D x F	D	F	D x F
Ash	-[6]	<0.001[5]	<0.001	-	<0.001	0.22	-	0.07	0.63	-	0.20	0.42
Ca c	-	<0.001	0.23	-	<0.009	0.78	-	0.022	0.81	-	0.025	0.54
Ca ct	-	0.002	0.031	-	0.62	0.77	-	0.64	0.55	-	0.015	0.42
Mg c	-	<0.001	0.47	-	0.007	0.18	-	0.71	0.71	-	0.59	1.00
Mg ct	-	0.010	0.017	-	0.73	0.70	-	0.53	0.93	-	0.63	0.73
Fe c	-	0.048	0.049	-	0.079	0.51	-	0.16	0.46	-	0.47	0.24
Fe ct	-	0.65	0.02	-	0.17	0.72	-	0.52	0.39	-	0.41	0.18
Mn c	-	0.040	0.96	-	0.54	0.98	-	0.69	0.34	-	0.96	0.48
Mn ct	-	0.13	0.76	-	0.99	0.98	-	0.58	0.56	-	0.84	0.93
Zn c	-	<0.001	0.072	-	<0.001	0.056	-	0.60	0.65	-	0.58	0.051
Zn ct	-	<0.001	0.004	-	0.052	0.35	-	0.54	0.47	-	0.53	0.065
Cu c	-	0.49	0.46	-	0.80	0.57	-	0.94	0.33	-	0.58	0.25
Cu ct	-	0.97	0.27	-	0.98	0.63	-	0.90	0.31	-	0.62	0.20
B c	-	<0.001	0.015	-	0.023	0.17	-	0.12	0.31	-	<0.001	0.015
B ct	-	0.031	0.039	-	0.49	0.73	-	0.64	0.20	-	0.68	0.68

[1,3,4,5] as in Table 4.4;

[2] D -drainage, F - fertilization; Degrees of freedom were: Drainage = 1, fertilization = 2, D x F = 2 and error = 11. [6] Not shown since it included blanket application of N_oPK.

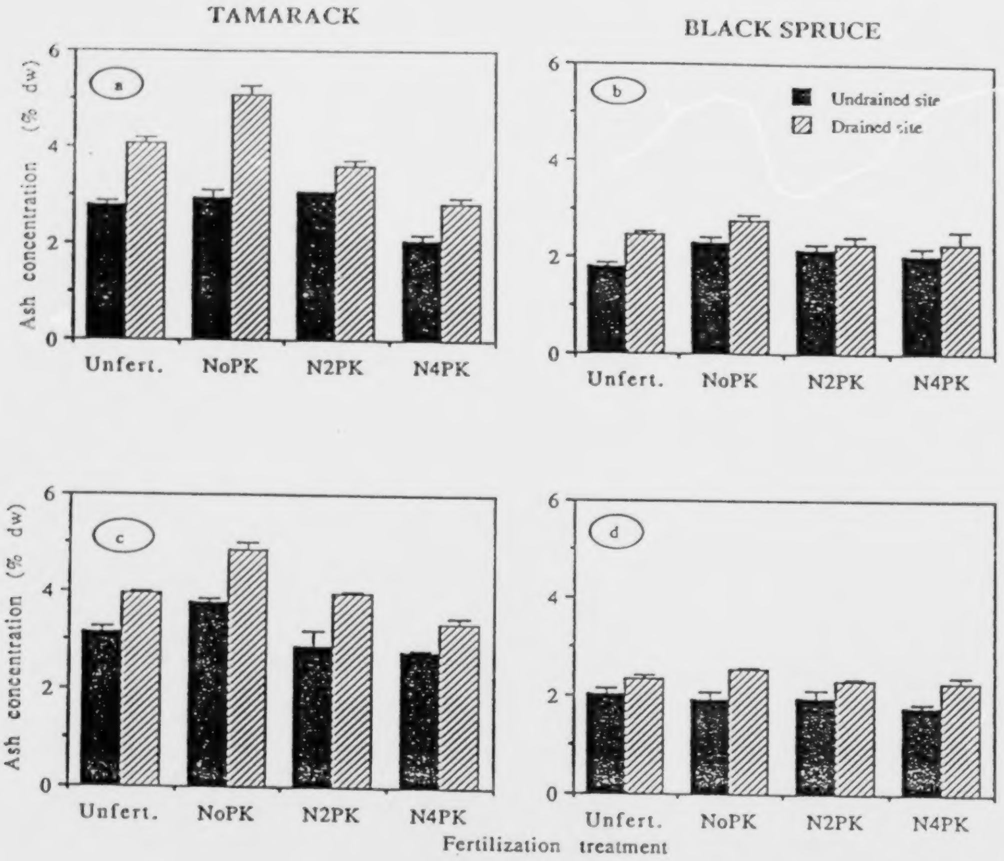


Figure 4.1: Effect of drainage and fertilization on foliar ash concentration of tamarack and black spruce (a and b - 1989; c and d - 1990) at Wolf Creek, central Alberta. Bars indicate standard errors of the mean of three plots.

followed the following sequence: Cu > Mn = Zn = Fe > Ca > Mg = B. However, in 1990 drainage resulted in vectors suggesting deficiency of all nutrients, except for Mg (Fig. 4.2a). The order of deficiency was as follows: Cu > Mn > Zn > Ca = Na > Fe = B. The effect of drainage was also significant (Table 4.4) for foliar Ca, Mg and Zn concentration in 1989, and Mg, Zn and B concentrations and contents for black spruce in 1990. Drainage resulted in excess nutrient concentrations and decreased unit needle mass of black spruce in both years (Fig. 4.2b). Increased growth of tamarack and black spruce in drained forested peatlands in central Alberta was associated with improved foliar N, P and S concentrations (Lieffers and Macdonald 1990).

Increased foliar nutrient concentrations may be related to increased nutrient supply due to enhanced rates of decomposition (Lieffers 1988) and mineralization of nutrients (Williams 1974; Williams and Wheatly 1988; Zhang and Liu 1991) related to favourable soil conditions. It is likely that drainage also increased rooting density (Lieffers and Rothwell 1987) and improved water relations of these trees, allowing greater nutrient uptake (Kozlowski 1982). In chapter 3 I theorized that decreased unit needle mass in black spruce may be related to preferential allocation of photosynthate to belowground than above ground due to initially high shoot/root ratio and limited supply of N.

4.3.2.2 Fertilization and its interaction with drainage

N_0PK significantly ($P<0.002$, Table 4.4) increased foliar ash concentration for tamarack in undrained and drained sites in both years and for black spruce in 1989 (Fig. 4.1a,c). This increase may be related to higher concentration and content of the main nutrients (Table 4.3) and silica (probably plant opal). Tamarack foliar samples from N_0PK plots had higher amounts of acid insoluble residue (following ashing of foliage and dissolution of ash in nitric and hydrochloric acid) than control that was identified as Si based on a semi-quantitative method using energy dispersive system of Scanning Electron Microscopy. N_0PK also increased ($P<0.05$) foliar B concentration for tamarack and black spruce. The interaction of N_0PK

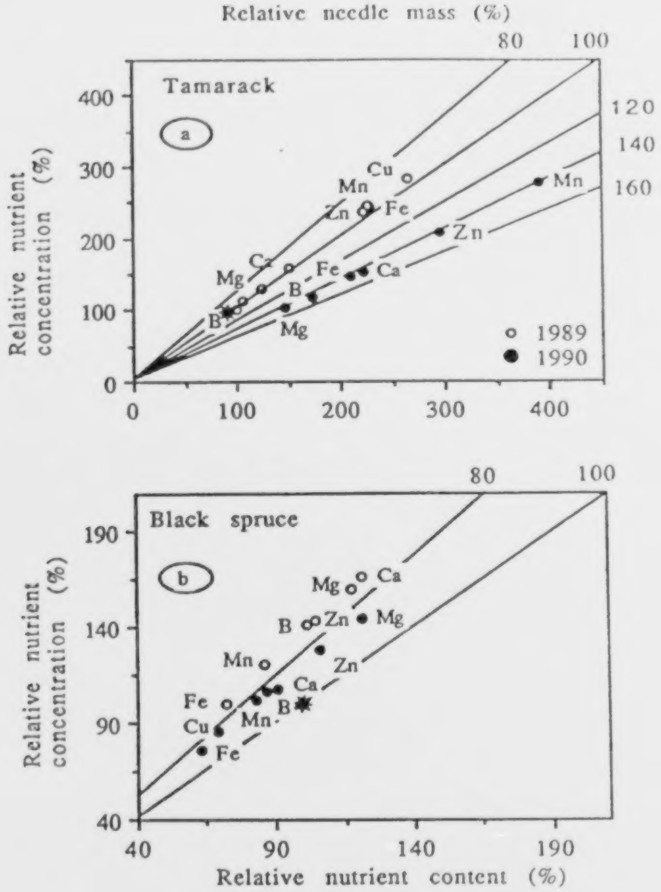


Figure 4.2: Effect of drainage on relative needle mass and foliar macro- and micro-nutrients of tamarack (a) and black spruce (b) sampled on 31 August in the second (1989) and on 2 September in the third (1990) growing seasons after ditching at Wolf Creek, central Alberta. Absolute mean unit needle mass, and foliar macro- and micro-nutrient concentrations and contents of tamarack and black spruce from undrained-unfertilized plots are given in Table 4.3. Star symbol represents foliar status of undrained-unfertilized plots (reference) - equalized to 100. Cu is partly displayed since relative concentration and content were respectively 327 and 470% for tamarack (1990), and respectively 555 and 426% for black spruce (1989). Vectors are not shown in order to avoid overcrowding.

and drainage significantly ($P<0.002$) increased foliar B concentration in black spruce in 1990 (Tables 4.3 and 4.4) with greater increase on the undrained relative to the drained site.

In general, urea fertilization changed foliar ash and nutrient concentrations and contents although the magnitude of change varied with species, drainage treatment and dosage of N-fertilizer (Table 4.4; Figs. 4.1, 4.3 and 4.4). For tamarack, urea fertilization decreased ($P<0.05$, Table 4.5) foliar ash concentration (Fig. 4.1), Zn (both years), Mg and Ca (1989) concentrations and contents, and Fe and Mn (1989), Mg and Ca (1990) concentrations (Fig. 4.3). There was a significant ($P<0.05$) drainage-by-fertilization interaction on foliar ash concentration, Fe, Zn and B concentrations and contents, Mg and Ca content (1989). Urea fertilization decreased foliar concentration of these nutrients with greater decrease on the drained site. Addition of N_4PK resulted in greater decrease in foliar nutrients than N_2PK on both sites. However, N_2PK increased Ca, Mg, Fe and B on the undrained site. For black spruce, urea fertilization decreased ($P<0.03$) foliar Ca (1989) and B (1990) concentrations, and Ca (1990) concentration and content. The drainage by N-fertilization interaction was significant ($P<0.02$) for foliar B concentration in 1990. The decrease in B concentration was greater in the undrained relative to the drained site. This decrease may be related to dilution since unit needle mass increased with urea fertilization.

For tamarack, urea fertilization increased foliar B (1989) and Fe (1990) in N_2PK- and for Cu (1990) in N_4PK-undrained plots; and for Mn (1990) concentration and content in the drained site for both N levels (Fig. 4.3). However, vectors associated with these nutrients suggest deficiency. These results suggest that urea increased availability and uptake or retranslocation of some nutrients relative to N_0PK. For black spruce, corresponding increases in the undrained site occurred for Mg (1989) and Fe (1990) (Fig. 4.4).

Decreased foliar nutrient concentrations induced by N-fertilization have been documented for several tree species such as for P, Ca, Mg, Mn, Fe and B (Gill and Lavender 1983); P, Mn, Fe and B (DeBell *et al.* 1975); Ca, Mg and P (Radwan and DeBell 1989) in *Tsuga heterophylla*; P, K, Mg and B in young and old pines (Paavilainen and Pietilainen 1983); Mn in young red spruce and balsam fir stand

Figure 4.3: Effect of drainage and urea dosage on relative needle mass and foliar macro- and micro-nutrients of tamarack sampled on 31 August in the second (1989) and on 2 September in third (1990) growing seasons after ditching at Wolf Creek, central Alberta. Absolute mean unit needle mass, and foliar macro- and micro-nutrient concentrations and contents of tamarack from undrained- and drained-NoPK plots are given in Table 4.3. Star symbol represents foliar status of undrained- and drained-NoPK plots (reference) - equalized to 100. Vectors are not shown in order to avoid overcrowding.

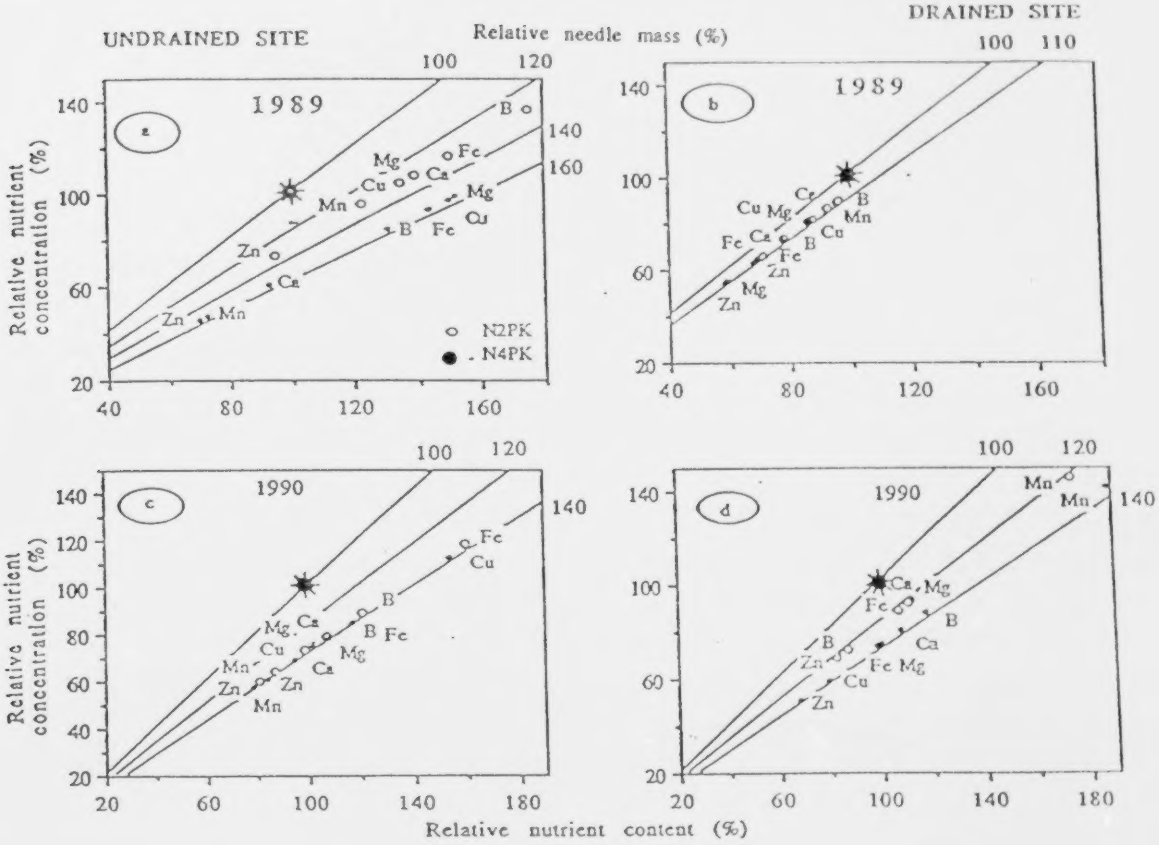
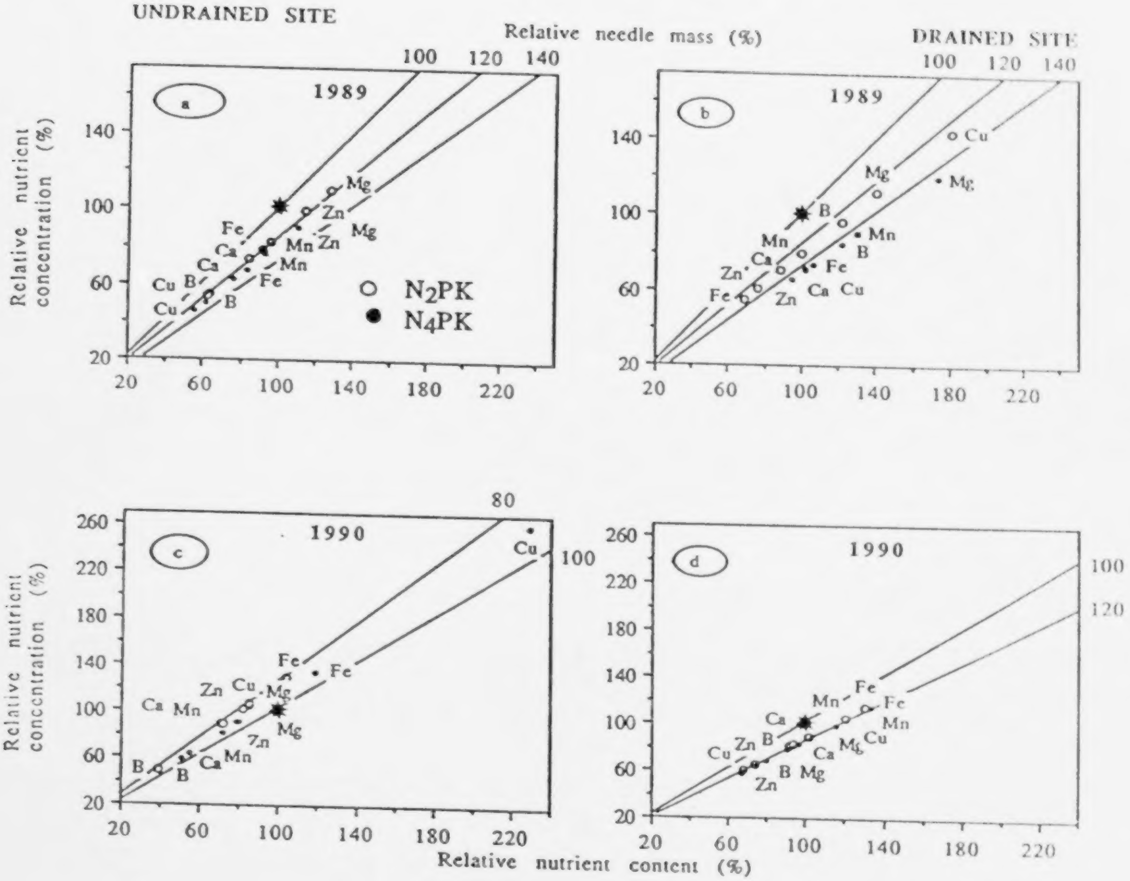

UNDRAINED SITE
Relative needle mass (%)
DRAINED SITE
a
1989
100
120
140
160
B
Fe
Mg
Ca
Cu
Mn
Zn
Mg
Cu
B
Fe
Ca
Zn
Mn
N2PK
N4PK
Relative nutrient concentration (%)
b
1989
100
110
Ca
B
Mn
Cu
Mg
Cu
Fe
Ca
Fe
B
Zn
Mg
Zn
c
1990
100
120
140
Fe
Cu
B
B
Fe
Mg
Ca
Mg
Cu
Ca
Mn
Zn
Zn
Mn
d
1990
100
120
140
Mn
Mn
Ca
Mg
Fe
B
B
Ca
Zn
Fe
Mg
Cu
Zn
20
40
60
80
100
120
140
160
180
Relative nutrient content (%)

Figure 4.4: Effect of drainage and urea dosage on relative needle mass and foliar macro- and micro-nutrients of black spruce sampled on 31 August in the second (1989) and on 2 September in third (1990) growing seasons after ditching at Wolf Creek, central Alberta. Absolute mean unit needle mass, and foliar macro- and micro-nutrient concentrations and contents of black spruce from undrained- and drained-NoPK plots are given in Table 4.3. Star symbol represents foliar status of undrained- and drained-NoPK plots (reference) - equalized to 100. Vectors are not shown in order to avoid overcrowding.


UNDRAINED SITE
Relative needle mass (%)
DRAINED SITE
100
120
140
a
1989
b
1989
c
1990
d
1990
80
100
120
Relative nutrient concentration (%)
Relative nutrient content (%)
N2PK
N4PK
Cu
B
Ca
Fe
Mn
Zn
Mg
20
60
100
140
180
220
260

(Czapowskyj *et al.* 1980); P and K in black spruce seedlings (Munson and Timmer 1989); and P and K in tamarack and black spruce (see chapter 3).

Some possible causes of reduced foliar nutrient concentration and content are summarized in chapter 3. Reduction of already low foliar levels of some essential nutrients due to N-fertilization may result in unbalanced foliar nutrient concentrations that may result in reduced growth response (Gill and Lavender 1983). For the present study, urea fertilization changed foliar nutrient balance of both species relative to that of unfertilized trees (Table 4.6). This may have caused the significant negative relationship between unit needle mass and foliar nutrients (Table 4.7). These results suggest that balanced fertilizers may be required to ensure balanced foliar nutrients for optimum tree productivity in drained central Alberta peatlands.

However, my reasoning does not explain the cause of decreased unit needle mass for black spruce in undrained urea plots in 1990. Since some mortality of black spruce was observed in 1990 on undrained, higher-dosage (400 kg $N.ha^{-1}$) urea plots, toxic effects of ammoniacal-N can not be ruled out. Toxic effects associated with ammoniacal-N are more evident in herbaceous plants grown in solution near neutral pH (Tolley-Henry and Raper 1986). Tamarack and black spruce trees on the undrained site may have different resistances to ammoniacal-N toxicity as inferred from the unit mass of tamarack being increased by urea.

4.4 CONCLUSIONS

As related to my original hypotheses:

a) Drainage had no effect on organic soil ash and elemental concentrations, except for Mn and Zn, and N during the first growing season following ditching. These results suggest that changes in elemental concentrations in peat associated with drainage do not take place within the first year.

Table 4.6: Percent of nutrient concentration[1] relative to nitrogen concentration in tamarack and black spruce foliage near the end of the third and second growing seasons following ditching and fertilization, respectively, at Wolf Creek, central Alberta.

		N	K	P	Ca	Mg	Fe	Mn	Zn	Cu	B
Sitka spruce[2]		100	55	16	4	4	0.7	0.4	0.03	0.03	0.2
Norway spruce[2]		100	50	16	5	5	0.7	0.4	0.03	0.03	0.2
Japanese larch[2]		100	60	20[3]	5	8.5	0.7	0.4	0.03	0.03	0.2
					Tamarack						
Undrained site	Unfer.	100	45	18	26	12	0.42	5	0.15	0.005	0.21
	N_0PK	100	49	27	29	12	0.47	6	0.16	0.01	0.20
	N_2PK	100	39	17	19	8	0.47	3	0.09	0.006	0.15
	N_4PK	100	36	15	17	8	0.33	3	0.08	0.001	0.14
Drained site	Unfer.	100	31	13	23	7	0.36	9	0.18	0.01	0.14
	N_0PK	100	44	29	24	6	0.37	5	0.18	0.011	0.17
	N_2PK	100	36	16	22	5	0.34	7	0.12	0.01	0.12
	N_4PK	100	24	10	16	4	0.23	5	0.07	0.005	0.12
					Black spruce						
Undrained site	Unfer.	100	74	17	42	11	0.35	9	0.51	0.014	0.23
	N_0PK	100	74	17	41	10	0.24	9	0.38	0.007	0.34
	N_2PK	100	58	14	28	8	0.25	7	0.31	0.006	0.13
	N_4PK	100	48	12	17	6	0.22	5	0.23	0.012	0.13
Drained site	Unfer.	100	66	15	33	11	0.20	7	0.48	0.008	0.18
	N_0PK	100	69	17	35	11	0.21	6	0.52	0.02	0.19
	N_2PK	100	61	12	23	7	0.20	5	0.28	0.01	0.13
	N_4PK	100	55	12	22	7	0.20	5	0.24	0.003	0.11

[1] Based on nutrient concentrations of foliar samples of 1990;

[2] Optimum nutrient concentration in whole seedling. Growing nutrient solution supplied to root system by misting (Ingestad 1979);

[3] Luxury consumption probably involved.

Table 4.7: Summary of Pearson correlation coefficients[1] describing the relationship between unit needle mass and foliar nutrient concentration in response to drainage and urea fertilization at Wolf Creek, central Alberta.

Species/ year	Ca	Mg	Fe	Mn	Zn	Cu	B
				Undrained site			
Tamarack							
1989	-0.586*[2]	-0.827*	0.016	-0.382	-0.862*	0.105	-0.276
1990	-0.146	-0.424	-0.557*	-0.064	-0.500*	0.136	-0.160
B. spruce							
1989	-0.355	-0.072	-0.249	0.095	-0.130	-0.169	-0.185
1990	0.122	0.019	0.055	-0.095	0.333	-0.273	0.522*
				Drained site			
Tamarack							
1989	0.739*	-0.723*	-0.632*	-0.606*	-0.805*	-0.329	-0.619*
1990	-0.553*	-0.613*	-0.655*	-0.270	-0.792*	-0.560*	-0.077
B. spruce							
1989	-0.501*	-0.344	-0.245	-0.105	-0.536*	0.113	-0.707
1990	-0.547*	-0.492	0.340	-0.338	-0.496*	-0.236	-0.403

[1] Based on unfertilized and fertilized trees;
[2] Significance indicated by * for $P \leq 0.05$.

b) Drainage, generally increased foliar nutrient concentrations and contents of tamarack and black spruce in both years. This may be related to improved soil conditions following drainage that may have enhanced rate of peat decomposition, nutrient uptake through increased transpiration and nutrient transport from roots to leaves. However, drainage did not alleviate sub-optimal foliar nutrient levels for black spruce that existed before ditching. Drainage also increased foliar ash content, with greater increase occurring for tamarack than for black spruce. This may be related with increased uptake of silicic acid with improved soil conditions.

c) N fertilization decreased foliar ash and some nutrient concentration for tamarack and black spruce probably due to dilution with greater decrease on the drained site. On the other hand, decrease in nutrient content in N fertilized plots may be related to reduced nutrient uptake. However, N fertilization increased Fe, Cu and B on the undrained site, and Mn on the drained site. These changes may result in foliar nutrient imbalances that may decrease growth as observed for black spruce on the undrained site in 1990. Thus, use of balanced nutrient fertilizer in drained and undrained peatlands in Alberta may be necessary in order to ensure balanced foliar nutrients for the two species.

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Chapter 5

PHOTOSYNTHESIS AND WATER RELATIONS RESPONSES OF TAMARACK AND BLACK SPRUCE TO DRAINAGE AND FERTILIZATION OF A MINEROTROPHIC PEATLAND.

5.1 INTRODUCTION

In chapters 3 and 4 I examined the effects of drainage and fertilization on foliar responses of tamarack and black spruce. In the present study, I examine the effects of drainage and fertilization on ecophysiological responses of tamarack (*Larix laricina* (Du Roi) K. Koch.) and black spruce (*Picea mariana* (Mill.) B.S.P.). Macdonald and Lieffers (1990) observed that drainage increased rates of net assimilation (NA), water-use efficiency (WUE), and mesophyll conductance (g_m) of peatland tamarack and black spruce. They attributed these initial physiological effects of drainage to the improvement of nitrogen relations. Drainage without fertilization increased foliar N and P concentrations and contents of tamarack and black spruce, but decreased unit needle mass of black spruce in central Alberta (chapter 3).

Drainage of peatlands in central Alberta did not increase foliar N and P concentrations of black spruce beyond the range of moderate deficiency (Macdonald and Lieffers 1990; Lieffers and Macdonald 1990; see chapters 2 and 3) as defined by Swan (1970) for black spruce seedlings grown in sand culture. For tamarack, foliar N and P concentrations in undrained and drained peatlands of central Alberta (Macdonald and Lieffers 1990; Lieffers and Macdonald 1990; see chapter 3) were within or above those reported for undrained peatlands (Small 1972), Minnesota fens (Tilton 1978) and a Wisconsin bog (Tyrrell and Boerner 1987).

I am not aware of any field study that evaluated foliar N and P concentrations for optimum growth of tamarack. Suboptimal levels of N and P may reduce both the photosynthetic capacity (see Kellomaki *et al.* 1982; Sheriff *et al.* 1986; Reich and Schoettle 1988) and water-use efficiency (van den Driessche 1972; Linder and Rook 1984) of conifers.

Addition of NPK to undrained and drained plots in a minerotrophic peatland in central Alberta significantly increased unit needle mass of tamarack and black spruce suggesting that the growth of these species was N limited (chapter 3). Fertilizer, as a readily available nutrient source, could increase foliage area and net assimilation rate, and change assimilate partitioning of tamarack and black spruce in recently drained peatlands. Increased soil nutrient availability by fertilization of natural peatlands may increase foliar N and P concentrations with a consequential improvement in ecophysiological performance and tree growth. Knowledge of interaction of drainage and fertilization upon carbon assimilation and water relations of peatland tamarack and black spruce of boreal western Canada is generally lacking.

In this chapter I examine the following hypotheses: a) drainage without fertilization increases net assimilation rate and related ecophysiological parameters, and improves resource (water and N) utilization efficiencies; b) addition of NPK improves ecophysiological performance with higher responses on the drained than on the undrained site; c) addition of NPK reduces photosynthetic N-use efficiency (PNUE) due to increase in foliar N concentration and improves WUE ; d) a trade-off exists between maximizing water- and N-use efficiencies; and e) the resource use efficiencies of deciduous tamarack are significantly different from those of evergreen black spruce.

5.2 MATERIALS AND METHODS

5.2.1 Study area and experimental design

The peatland soil and stand characteristics and experimental design are documented in detail in chapter 3.

5.2.2 Foliar gaseous exchange

Gaseous exchange measurements and foliar sampling were simultaneously carried out on each of the 24 plots (12 each in undrained and drained sites) in 1989 and 1990 as follows: a) 1989, 28 June and 4 July (tamarack) and 16 and 17 August (black spruce) when current needles were fully developed, and b) 1990, 11 and 12 August.

A portable gas exchange system for the simultaneous measurement of CO_2 uptake, relative humidity, temperature and photosynthetically-active radiation (PAR) (LCA-2, air pump, and cuvette PLC-C, Analytical Development Corporation, Hoddeson, England) was used as described by Macdonald and Lieffers (1990). Predried ambient air (4-6% relative humidity) was pumped into the cuvette at a rate of 10 (1989) or 8 (1990) mL s^{-1}. With the tissue in place relative humidity in the cuvette was 25 - 50%. During cloudy periods in 1989 natural light was supplemented by a Brinkman 'Q-beam' spotlight positioned to supply 1600 uE.m^{-2}.s^{-1} and in 1990 it was supplemented by a 20 W, 12 v Tungsten Halogen lamp positioned to supply 1200 uE.m^{-2}.s^{-1}. Macdonald and Lieffers (1990) observed that these light intensities were well above the light intensity for saturation of photosynthesis in these tree species (ca 700 uE.m^{-2}.s^{-1}). Rates of carbon assimilation (NA, $u$mol $CO_2.m^{-2}.s^{-1}$), stomatal conductance to H_2O vapor (g_s, $u$mol $H_2O.m^{-2}.s^{-1}$), mesophyll conductance to CO_2 (g_m, $u$mol $CO_2.m^{-2}.s^{-1}$) and instantaneous photosynthetic water-use efficiency ($u$mol CO_2 fixed per mmol H_2O transpired) were determined using standard calculations (Caemmerer and Farquhar 1981). Instantaneous photosynthetic nitrogen-use efficiency ($u$mol CO_2 fixed per g of foliar N) was calculated according to Evans (1989). Because the air in the leaf chamber was well-mixed, leaf conductance was considered to be representative of stomatal conductance. Leaf temperature was assumed to be the same as air temperature in the cuvette.

For each species, three fully exposed and apparently healthy trees were randomly selected from each of the 12 plots on the undrained site and on the drained site (i.e., for each species: 3 trees x 4 fertilization treatments (unfertilized, N_0PK, N_2PK, N_4PK) x 3 plots x 2 sites (undrained, drained)). Photosynthesis was measured in the field on attached branchlets at 1 to 1.5 m above ground level between 0900 and 1400 h (M.S.T.) in 1989, and between 0800 and 1600 h in 1990. For tamarack, a single branchlet with short-shoots of various stem ages was selected. For black spruce in 1989, current-year and one-year-old tissues were combined in order to have enough needle mass while in 1990, current-year needles were sufficient. In 1989, each plot was visited six times and on each visit one of the selected trees was randomly chosen and measured. In 1990, each plot was visited three times, and on each visit one tree of each species was measured. The order in which plots were visited was randomized. Mean air temperature in the cuvette on 28 June, 4 July, and 16 and 17 August 1989 was respectively 21.8, 26.0, 22.2 and 20.4 ^{o}C.; and on 11 and 12 August 1990 was respectively 30.6 and 31.7^{o}C. The allometric needle area-mass equations developed by Macdonald and Lieffers (1990) for tamarack and black spruce from another peatland were used to estimate needle area from dry weight.

5.2.3 Foliar analysis

Foliar samples of the photosynthesis branchlets were dried at 65^{o}C for 24 h and allowed to equilibrate at room temperature and humidity before needle separation and weighing. Dry needles were ground, digested and analysed for N and P as described in chapter 2. Mean deviations from the reference National Institute of Standards and Technology No. 1575 orchard leaves means were a relative -0.11% for N and - 0.01% for P using one reference per 15 foliar samples.

5.2.4 Data analysis

Analysis of variance (ANOVA) and analysis of covariance (ANCOVA) were carried out with the aid of a microcomputer using the general linear model (GLM) procedure of SAS (SAS Inst. Inc. 1987). For each sampling year (1989 and 1990), data were sorted into two subsets according to the following groupings of fertilizer treatments: a) unfertilized and N_0PK, and b) N_0PK, N_2PK and N_4PK. The second grouping was to isolate the effect of N fertilization from that of N_0PK. Each subset was separately subjected to the following analyses. The null hypothesis for homogeneity of variance for each error term was tested by the Shapiro-Wilk procedure (SAS Inst. Inc. 1987). I found only moderate violations of assumptions of homogeneity which are known to have little effect given the robustness of the F-ratio test (Winer 1971). Thus, no data transformations were utilized. The ANOVA and ANCOVA models tested for effects of drainage, fertilization and their interaction upon the ecophysiological responses. The covariates used for analysis of the ecophysiological responses were: time of the day, cuvette air temperature, and PAR as suggested by Macdonald and Lieffers (1990).

The pooled data were sorted by year, species and drainage. Thereafter, data for each species from each site per year were separately subjected to Pearson correlation analysis to: a) determine the relationship between ecophysiological parameters; and b) use orthogonal polynomials to check for linear and quadratic response of each ecophysiological parameter to N_0PK, N_2PK and N_4PK (Steel and Torrie 1980).

5.3 RESULTS

5.3.1 Tamarack

5.3.1.1 Drainage

For tamarack in 1989, drainage (without fertilization) did not affect net assimilation rate (NA), stomatal conductance to H_2O vapor (g_s), mesophyll conductance to CO_2 (g_m), instantaneous photosynthetic N-use efficiency (PNUE) or foliar P concentration (Table 5.1). In contrast, trees on drained plots showed significantly greater water-use efficiency (WUE) and foliar N concentration (Table 5.2). However, in 1990 drainage significantly increased NA, g_m, WUE and foliar N and P, and decreased PNUE (Tables 5.1 and 5.2).

5.3.1.2 Fertilization and its interaction with drainage

In 1989, N_0PK did not affect most parameters measured except for a foliar P concentration increase (Table 5.1), and this increase was

Table 5.1: Probability values from ANCOVA and ANOVA (N and P) of ecophysiological responses of tamarack and black spruce to drainage and N_oPK fertilization at Wolf Creek, central Alberta.

	NA[a]	g_s	g_m	WUE	PNUE	N	P
				1989			
Tamarack							
Drain.[b]	0.27	0.13	0.10	0.008	0.27	<0.001	0.16
Fert.	0.48	0.72	0.44	0.26	0.43	0.72	<0.001
DxF	0.97	0.47	0.65	0.94	0.93	0.98	0.015
Black spruce							
D	0.020	0.036	0.081	0.57	0.005	0.003	<0.001
F	0.37	0.37	0.69	0.60	0.82	0.46	<0.001
DxF	0.85	0.50	0.94	0.91	0.73	0.80	0.33
				1990			
Tamarack							
D	0.007	0.69	<0.001	<0.001	0.004	<0.001	0.023
F	0.010	0.070	0.006	0.17	0.046	0.49	<0.001
DxF	0.40	0.84	0.19	0.12	0.52	0.66	0.12
Black spruce							
D	0.039	0.89	0.016	0.003	0.85	<0.001	<0.001
F	0.73	0.11	0.40	0.13	1.00	0.40	<0.001
DxF	0.99	1.00	0.72	0.70	0.72	0.81	0.014

[a] NA - net assimilation rate (μmol $CO_2.m^{-2}.s^{-1}$); g_s - stomatal conductance to water vapor (μmol $H_2O.m^{-2}.s^{-1}$); g_m - mesophyll conductance to CO_2 (μmol $CO_2.m^{-2}.s^{-1}$); WUE - photosynthetic water-use efficiency (μmol CO_2 fixed/mmol H_2O transpired); PNUE - photosynthetic N-use efficiency (μmol $CO_2.(g\ N)^{-1}.s^{-1}$); N and P are foliar concentration (%) on mass basis;

[b] Drain - drainage, Fert - fertilization; Degrees of freedom for Drain, Fert, D x F and Error are respectively 1,1,1 and 32; and for each covariate is 1. Fertilization treatments were unfertilized and N_oPK at 0-80-120 $kg.ha^{-1}$;

Table 5.2: Ecophysiological responses of tamarack to drainage and fertilization at Wolf Creek, central Alberta.

Response variable[1]	Year	Undrained site						Drained site					
		Unfert.	N_0PK	N_2PK	N_4PK	Polynom.[2]		Unfert.	N_0PK	N_2PK	N_4PK	Polynom.	
						L	Q					L	Q
NA	1989	1.65[3] (0.07)	1.68 (0.08)	1.73 (0.11)	1.43 (0.10)	0.083[4]	0.18	1.79 (0.08)	1.87 (0.17)	1.58 (0.13)	1.40 (0.20)	0.055	0.81
	1990	1.41 (0.17)	1.71 (0.13)	1.41 (0.18)	1.32 (0.22)	0.008	0.26	1.78 (0.17)	1.97 (0.17)	1.64 (0.13)	1.51 (0.10)	0.010	0.57
g_s	1989	38.81 (2.35)	39.76 (2.29)	37.30 (2.05)	36.46 (2.46)	0.33	0.83	37.99 (2.35)	37.36 (2.82)	32.41 (3.61)	30.20 (4.44)	0.16	0.80
	1990	24.90 (2.17)	27.40 (1.82)	22.65 (1.94)	22.51 (2.11)	<0.008	0.19	24.93 (2.02)	28.53 (3.01)	21.98 (1.76)	22.20 (1.77)	0.059	0.27
g_m	1989	6.41 (0.26)	6.45 (0.33)	6.63 (0.46	5.43 (0.43)	0.092	0.10	7.04 (0.29)	7.61 (0.73)	6.44 (0.52	5.63 (0.77)	0.050	0.87
	1990	6.01 (0.75)	7.50 (0.65)	6.12 (0.79)	5.44 (0.92)	0.014	0.40	8.20 (0.83)	9.03 (0.69)	7.94 (0.60)	6.92 (0.43)	0.007	0.93
WUE	1989	1.92 (0.08)	2.07 (0.12)	2.23 (0.08)	1.82 (0.18)	0.21	0.10	2.63 (0.28)	2.82 (0.39)	2.33 (0.20)	2.23 (0.32)	0.070	0.51
	1990	1.58 (0.19)	1.89 (0.14)	2.10 (0.32)	2.17 (0.46)	0.40	0.78	2.46 (0.21)	2.27 (0.21)	2.36 (0.11)	2.20 (0.18)	0.89	0.008
PNUE	1989	3.97 (0.17)	4.09 (0.14)	2.98 (0.17)	2.29 (0.19)	<0.001	0.35	3.76 (0.18)	3.95 (0.44)	2.14 (0.09)	2.10 (0.34)	<0.001	0.032
	1990	3.42 (0.38)	3.89 (0.33)	2.69 (0.32)	2.44 (0.38)	<0.001	0.021	2.64 (0.26)	2.91 (0.29)	2.25 (0.18)	1.80 (0.12)	<0.001	0.71
N	1989	1.51 (0.04)	1.50 (0.03)	2.11 (0.04)	2.27 (0.10)	<0.001	0.014	1.74 (0.06)	1.73 (0.05)	2.69 (0.09)	2.43 (0.09)	<0.001	<0.001
	1990	1.53 (0.09)	1.61 (0.07)	1.91 (0.11)	1.94 (0.10)	0.025	0.32	2.47 (0.06)	2.49 (0.07)	2.65 (0.05)	3.05 (0.09)	<0.001	0.28
P	1989	0.24 (0.01)	0.30 (0.01)	0.20 (0.01)	0.21 (0.01)	<0.001	0.003	0.22 (0.01)	0.35 (0.02)	0.27 (0.01)	0.22 (0.01)	<0.001	0.20
	1990	0.27 (0.03)	0.42 (0.05)	0.25 (0.03)	0.24 (0.02)	0.003	0.077	0.30 (0.01)	0.56 (0.04)	0.37 (0.01)	0.32 (0.02)	<0.001	0.069

[1] As defined in Table 5.1;

[2] Orthogonal polynomial contrasts, L - linear relation, Q - quadratic relation, within drainage levels;

[3] Mean of 9 observations with standard error in parentheses;

[4] P>F, degree of freedom for each contrast = 1.

more pronounced on the drained site (Table 5.2). In 1990, N_0PK increased NA and g_m on the undrained site and foliar P for both sites (Tables 5.1 and 5.2). Overall trends were that the drained-N_0PK plots had the highest values for most of these variables owing to the combined effect of drainage and N_0PK fertilization.

In 1989 and 1990, N fertilization significantly decreased NA, g_m, PNUE and foliar P with a greater decrease occuring in N_4PK plots (Tables 5.2 and 5.3). Foliar N concentration significantly increased between N_0PK and N_2PK on the undrained site and to N_4PK on the drained site, in both years. In 1990, these variables were a linear function of N dose on both sites.

5.3.2 Black spruce

5.3.2.1 Drainage

For black spruce in 1989, drainage significantly increased NA, g_s, PNUE, foliar N and P concentrations (Tables 5.1 and 5.4). In 1990, significant increases occurred in NA, g_m, WUE, and foliar N and P with drainage.

5.3.2.2 Fertilization and its interaction with drainage

In 1989 and 1990, N_0PK significantly increased only foliar P concentration on both undrained and drained plots (Table 5.1). In both years, N fertilization resulted in higher foliar N concentrations in black spruce on the drained as well as undrained sites (Table 5.4). However, N_2PK or N_4PK generally lowered PNUE and P concentration for both sites compared to N_0PK. Generally, significant linear relationships prevailed between N dosages and PNUE and N on both sites in 1989 and 1990 (Table 5.4).

Table 5.3: Probabiliy values for ANCOVA and ANOVA (N and P) of ecophysiological responses of tamarack and black spruce to drainage and N_0PK, N_2PK and N_4PK fertilization at Wolf Creek, central Alberta.

	NA[a]	g_s	g_m	WUE	PNUE	N	P
				1989			
Tamarack							
Drain.[b]	-[d]	-	-	-	-	-	-
Fert.	0.025	0.18	0.023	0.068	<0.001	<0.001	<0.001
D x F	0.48	0.78	0.40	0.22	0.38	0.016	0.15
Black spruce							
D	-	-	-	-	-	-	-
F	0.67	0.13	0.65	0.86	0.003	<0.001	0.017
DxF	0.95	0.71	0.70	0.27	0.75	0.49	0.26
				1990			
Tamarack							
D	-	-	-	-	-	-	-
F	0.001	0.002	0.002	0.19	<0.001	<0.001	<0.001
D x F	0.93	0.90	0.79	0.69	0.62	0.10	0.57
Black spruce							
D	-	-	-	-	-	-	-
F	0.10	0.30	0.10	0.33	<0.001	<0.001	<0.001
D x F	0.99	0.62	0.96	0.88	0.719	0.109	0.001

[a] As defined in Table 5.1;

[b] Drain - drainage, fert - fertilization; Degrees of freedom for Drain, Fert, DxF and Error are respectively 1,1, 2 and 45; and for each covariate is 1.

[d] Not shown since it involves blanket application of N_0PK.

Table 5.4: Ecophysiological responses of black spruce to drainage and fertilization at Wolf Creek, central Alberta.

Response variables^1	Year	Undrained site						Drained site					
		Unfert.	NOPK	N2PK	N4PK	Polynom.^{2}		Unfert.	NOPK	N2PK	N4PK	Polynom.	
						L	Q					L	Q
NA	1989	1.72^3 (0.17)	1.58 (0.19)	1.65 (0.21)	1.46 (0.13)	0.66^4	0.67	2.08 (0.10)	1.97 (0.10)	1.85 (0.18)	1.71 (0.23)	0.51	0.89
	1990	1.42 (0.23)	1.46 (0.14)	1.26 (0.27)	1.20 (0.27)	0.25	0.84	1.84 (0.18)	1.67 (0.19)	1.50 (0.23)	1.41 (0.14)	0.097	0.88
g_s	1989	48.43 (4.79)	55.15 (3.00)	51.16 (3.29)	43.46 (3.11)	0.018	0.65	60.74 (4.40)	61.71 (4.13)	60.51 (5.44)	56.89 (4.79)	0.47	0.87
	1990	28.14 (2.93)	25.40 (1.61)	22.90 (2.84)	23.60 (1.67)	0.27	0.60	30.02 (1.93)	23.83 (2.21)	24.27 (1.90)	21.45 (1.28)	0.19	0.33
g_m	1989	6.09 (0.72)	5.78 (0.89)	6.49 (0.70)	5.65 (0.63)	0.98	0.54	7.57 (0.39)	7.16 (0.97)	7.09 (1.23)	5.86 (1.18)	0.31	0.78
	1990	6.12 (1.07)	6.37 (0.71)	5.56 (1.36)	4.54 (1.05)	0.27	0.60	8.16 (0.95)	8.19 (1.05)	7.31 (1.35)	6.57 (0.70)	0.082	0.78
WUE	1989	1.98 (0.18)	1.82 (0.23)	2.09 (0.21)	2.19 (0.23)	0.31	0.71	2.07 (0.21)	1.99 (0.29)	1.94 (0.27)	1.55 (0.22)	0.23	0.65
	1990	1.32 (0.21)	1.54 (0.18)	1.40 (0.24)	1.24 (0.20)	0.26	0.60	1.84 (0.21)	1.87 (0.24)	1.63 (0.30)	1.74 (0.23)	0.22	0.77
PNUE	1989	1.83 (0.15)	1.77 (0.24)	1.19 (0.27)	0.95 (0.23)	0.033	0.46	2.11 (0.09)	1.95 (0.21)	1.10 (0.37)	0.96 (0.33)	0.033	0.16
	1990	1.78 (0.28)	1.82 (0.16)	1.33 (0.29)	0.93 (0.24)	0.010	0.98	1.90 (0.24)	1.66 (0.15)	1.18 (0.19)	1.09 (0.11)	0.002	0.33
N	1989	0.80 (0.03)	0.84 (0.05)	1.30 (0.08)	1.45 (0.06)	<0.001	0.30	0.93 (0.02)	0.95 (0.03)	1.59 (0.10)	1.68 (0.07)	<0.001	0.007
	1990	0.78 (0.02)	0.80 (0.03)	0.98 (0.05)	1.20 (0.06)	<0.001	0.85	0.96 (0.03)	0.99 (0.04)	1.30 (0.06)	1.31 (0.05)	<0.001	0.007
P	1989	0.13 (<0.01)	0.15 (<0.01)	0.15 (0.01)	0.13 (0.01)	0.026	0.46	0.16 (0.01)	0.20 (0.01)	0.16 (0.01)	0.17 (0.01)	0.062	0.21
	1990	0.12 (<0.01)	0.14 (<0.01)	0.13 (0.01)	0.15 (0.01)	0.21	0.089	0.16 (0.02)	0.18 (0.01)	0.14 (<0.01)	0.14 (0.01)	<0.001	<0.001

[1,2,3,4] As defined in Table 5.2.

5.3.3 Determinants of NA and water relations

5.3.3.1 Tamarack

For tamarack in 1989 and 1990, NA was significantly positively correlated with WUE, g_s, g_m and PNUE on both sites, and inversely correlated with foliar N concentration on the drained site (Table 5.5). With the exception of WUE in 1990, WUE, g_s and g_m were significantly negatively correlated with foliar N concentration of tamarack on the drained site in both years. These correlations were not significant for the undrained site, except WUE and foliar N were positively correlated in 1990. NA was positively correlated with foliar P concentration on the undrained site in 1989 and on the drained site in 1990. WUE and g_m were positively correlated on both sites in both years. WUE and PNUE were positively correlated for the undrained site. PNUE of tamarack was negatively correlated with foliar N but positively correlated with foliar P on the undrained site in 1989 and the drained site in 1990.

5.3.3.2 Black spruce

NA of black spruce was significantly positively correlated with WUE, g_s, (except on the drained site, 1989) g_m and PNUE on both sites in 1989 and 1990 (Table 5.5). There was no significant relationship between NA and foliar N and P. On both sites and in both years WUE and g_s of black spruce were significantly positively correlated with g_m and PNUE (except g_s on the drained site, 1989). Foliar N and g_m were not related in black spruce. WUE was positively related to g_s in 1990 on the undrained site, and was inversely related to g_s on the drained site in 1989; otherwise the two variables were unrelated. The PNUE of black spruce was negatively correlated with foliar N concentration in both sites and in 1989 and 1990.

Table 5.5: Pearson correlation coefficients[a] describing the relationship among net assimilation rate (NA), photosynthetic water use efficiency (WUE), stomatal conductance (g_s), mesophyll conductance (g_m), photosynthetic nitrogen use efficiency (PNUE), and foliar N and P concentration[b] for tamarack and black spruce from undrained and drained sites. Correlation coefficients above and below diagonals are, respectively, for undrained and drained sites.

	1989							1990						
	NA	WUE	g_s	g_m	PNUE	N	P	NA	WUE	g_s	g_m	PNUE	N	P
Tamarack														
NA	1	0.536*^{c,d}	0.649*	0.965*	0.691*	-0.2039	0.3115*	1	0.765*	0.795*	0.958*	0.853*	0.198	0.204
WUE	0.632*	1	-0.062	0.558*	0.327*	-0.085	0.042	0.335*	1	0.534*	0.656*	0.520*	0.388*	-0.063
g_s	0.834*	0.529*	1	0.479*	0.540	-0.206	0.343*	0.907*	0.172	1	0.644*	0.751*	0.079	0.295*
g_m	0.971*	0.627*	0.781*	1	0.645*	-0.176	0.247	0.959*	0.289*	0.772*	1	0.786*	0.230	0.246
PNUE	0.709*	0.237	-0.526*	-0.572*	1	-0.825*	0.580*	0.940*	0.225	0.862*	0.901*	1	-0.319*	0.093
N	-0.374*	-0.294*	-0.340*	-0.395*	0.158	1	-0.485*	-0.306*	0.094	-0.296*	-0.307*	-0.597*	1	0.147
P	0.161	0.109	0.051	0.297*	-0.165	-0.094	1	0.3048	-0.089	0.334*	0.306*	0.278*	-0.111	1
Black spruce														
NA	1	0.704*	0.624*	0.994*	0.719*	-0.034	-0.036	1	0.883*	0.739*	0.976*	0.938*	-0.168	-0.028
WUE	0.675*	1	0.101	0.727*	0.638*	-0.233	0.050	0.806*	1	0.503*	0.878*	0.861*	-0.204	-0.088
g_s	0.080	-0.516*	1	0.562*	0.603*	-0.211	0.230	0.616*	0.246	1	0.620*	0.685*	-0.181	-0.075
g_m	0.984*	0.756*	-0.037	1	0.661*	0.125	0.023	0.963*	0.828*	0.429*	1	0.943*	-0.212	-0.035
PNUE	0.754*	0.557*	0.156	0.744*	1	-0.673*	-0.130	0.897*	0.643*	0.622*	-0.340*	1	-0.447*	-0.172
N	-0.199	-0.215	-0.159	-0.203	-0.765*	1	0.094	-0.188	-0.030	-0.150	0.143	-0.563*	1	0.606
P	0.183	0.069	0.127	0.138	0.251	-0.191	1	0.108	0.183	0.087	0.064	0.145	-0.168	1

[a] Based on unfertilized and fertilized trees;

[b] During the period of photosynthesis measurement;

[c] Significance indicated by * for $P \leq 0.05$;

[d] Mean of 9 observations.

5.4 DISCUSSION

5.4.1 Effect of drainage

Drainage without fertilization improved ecophysiological performance and nutrient relations of tamarack and black spruce. These results coincide with those of Macdonald and Lieffers (1990) for 4 years after ditching. My study suggests that these changes occur quickly (2-3 years) after drainage. An increase in foliar N and P concentrations in drained plots may be related to increased mineralization (Williams, 1974; Williams and Wheatley 1988), uptake and transport (Shapiro *et al.* 1956; Smith *et al.* 1989) of N and P from roots and leaves due to improved soil water, soil temperature and soil aeration relations.

Improved NA associated with drainage may be primarily due to increased g_m. A comparison of correlation coefficients among ecophysiological parameters in this study supports this reasoning since NA was more strongly correlated with g_m than other parameters. This increase in NA may be related to increased efficiency of carboxylation due to increased electron transport capacity and/or increased activity of the ribulose-1, 5-bisphosphate carboxylase (RUBISCO) (Benner *et al.* 1988).

There was no evidence that drainage improved tree water relations (g_s) except for black spruce in 1989. This conclusion agrees with that of Macdonald and Lieffers (1990). In both cases the period since drainage (ditching) may not have been sufficient for full adjustment of the root system to the new water table level and resulting thicker, more aerated profile. Drainage generally decreased PNUE of tamarack, but had no effect on that of black spruce in 1990, these results being consistent with those of Macdonald and Lieffers (1990). Decrease in PNUE for tamarack in my study may be related to a 61% (1990) increase in foliar N. In contrast, foliar N in black spruce increased modestly (16 and 21%), but was still within the range for moderate deficiency for black spruce seedlings grown in sand cultures (Swan 1970). Unit needle mass of tamarack was also decreased by drainage (see chapter 3).

5.4.2 Effect of fertilization and its interaction with drainage

I am not aware of other studies dealing with effects of the interaction of drainage and fertilization on ecophysiology of tamarack and black spruce. However, NA responses of conifers and broadleafed trees to drainage/flooding and fertilization separately are known. NPK fertilization has had variable effects on NA of different tree species. In my study N_0PK had no effect on any ecophysiological parameter of tamarack in the first year or in either year for black spruce. However, in 1990 N_0PK increased NA, g_s, g_m and foliar P concentration in tamarack. An effect of increased foliar P on these ecophysiological parameters is also revealed by some positive correlations with NA, g_s and g_m. Possible effects of P deficiency on photosynthesis may be: a) diminished photosynthesis by decreasing RUBISCO regeneration (Brooks 1986; Brooks *et. al.* 1988; Rao and Terry 1989), and b) altered ADP-ATP energy transfer system (Mulligan 1989).

In my study addition of NPK on undrained and drained sites had either no effect or decreased NA, g_s and g_m; and had no effect on WUE despite increases in foliar N and P. Other studies showed that N fertilization in the range of 80 and 400 kg $N.ha^{-1}$ increased NA of several upland conifers (Sheriff *et al.* 1986; Brix 1981; Miller and Miller 1976; Kellomaki *et al.* 1982) although, doses of over 450 kg $N.ha^{-1}$ decreased NA for several tree species (Miller and Miller 1976; Keller 1972 cited by Brix 1981; Brix 1981). My results are consistent with those for *Pinus elliottii* (van den Driessche 1972) and for several nonvascular and vascular plants in Alaska (Bigger and Oechel 1981). The decrease in NA following NPK fertilization may indicate lower enzyme concentrations and/or lower protein turnover rates at higher foliar N levels and/or dilution of essential nutrients other than nitrogen (Bigger and Oechel 1981).

In my study decreased NA of tamarack associated with N addition does not necessarily mean that there was reduced net carbon gain. This is because unit needle mass of tamarack in both sites and that of black spruce in the drained site in both years were increased by N addition (chapter 3). N fertilization may contribute to greater total canopy photosynthesis through increased allocation to leaf production even when NA has decreased (Bigger and Oechel 1982; Linder and Axelsson 1982; Oechel *et al.* 1981).

My findings of decreased g_s of tamarack in 1990 in N fertilized plots coincides with results for pines (Hellkvist *et al.* 1980 cited by Linder and Rook 1984; Linder and Troeng 1980; van den Driessche 1972). Decreased g_s may be due in part to lower stomatal densities per unit leaf area in the fertilized trees (Hellkvist *et al.* 1980). My finding that WUE was not improved by N fertilization may be related to decreased NA with N fertilization. Improved WUE after N or K addition has been reported for a wide range of coniferous species (Bradbury and Malcom 1977; Sheriff *et al.* 1986). In contrast, increased foliar N concentration decreased WUE of *Picea abies* (Keller 1970 cited by Linder and Rook 1984).

PNUE of tamarack and black spruce decreased with N fertilization, with N_4PK causing the greater decrease. This may be related to lower NA and higher foliar N concentration in N fertilized plots. This could be related to: a) finite liquid phase and cell wall conductance that would result in declining CO_2 concentration at the site of carboxylation with increasing weight-based photosynthetic capacity; b) a lower P:N ratio; or c) an increase in proportion of leaf N allocated to structural or defensive compounds rather than a photosynthetic function (Reich *et al.* 1989). On the undrained site, my foliar N:P ratio of N_0PK fertilized tamarack increased from 4:1 to 10:1 in N_4PK plots, and on the drained site from 5:1 to 8:1. For black spruce, corresponding ratios were 6:1 and 8:1 (undrained), and 6:1 and 9:1 (drained). Ingestad (1979) suggested an N:P ratio of 6:1 for optimum growth of *Picea* whole seedlings.

Addition of urea on the undrained plots increased foliar N and P above those of drained-unfertilized plots but there was no corresponding effect on ecophysiological parameters. Perhaps trees on the undrained site could not take advantage of improved foliar nutrients because of other limitations such as cold soil, poor aeration and flooding.

5.4.3 WUE vs PNUE

WUE and PNUE were positively correlated in both years for tamarack on the undrained site and for black spruce on both sites. This relationship was stronger on the undrained than on the drained site. Thus no trade-off seemed to occur between maximization of WUE and PNUE. Both species maximized water- and N-use efficiency at the same time. A trade-off of WUE and PNUE occurred in *Ulmus americana* on dry and wet sites (Reich *et al.* 1989), a response attributed to the unique coupling and feedback of the photosynthetic and transpiration processes, and because of the CO_2 dependence of photosynthetic rates. Maximization efficiency of use of water and N by tamarack and black spruce might be an adaptive mechanism to poor nutrient availability, cold soil and poor aeration associated with high water table levels.

5.4.4 Tamarack vs black spruce

Comparison of NA between tamarack and black spruce is questionable in 1989 due to the asynchronous measurements. In general NA (needle surface area basis) was similar for the two species in 1989 and in 1990 on the undrained site. For comparison with other studies, NA was expressed on a needle mass basis (Table 5.6). Expressed this way NA of tamarack is three to four times higher than that of black spruce. A similar magnitude of difference in NA occurred between larch and spruce species (Matyssek 1986). Tamarack's higher leaf nitrogen concentration and higher projected leaf area per unit dry mass does explain this difference.

I found similar g_m for both tamarack and black spruce. Small (1972) hypothesized that the greater compaction (packing density of mesophyll cells) of evergreen needles, such as black spruce, reduces g_m and hence decreases NA. Without fertilization tamarack had higher WUE and PNUE than black spruce. The greater utilization efficiency of nitrogen and water likely contributes to the survival of the deciduous tamarack in peatland sites.

Table 5.6: Effect of drainage and fertilization on net assimilation rate per unit dry mass (*u*mol $CO_2.g^{-1}.h^{-1}$) of tamarack and black spruce needles in 1989 and 1990.

Fertilization	1989		1990	
treatment	Undrained	Drained	Undrained	Drained
		Tamarack		
Unfertilized	216	234	184	232
N_0PK	220	246	224	257
N_2PK	226	207	184	214
N_4PK	188	183	173	198
Mean	213	218	191	225
		Black spruce		
Unfertilized	58.4	70.5	50.9	65.9
N_0PK	53.6	66.8	52.3	59.8
N_2PK	55.9	62.7	45.0	53.6
N_4PK	49.6	58.0	43.0	50.5
Mean	54.4	64.5	47.8	57.5

5.5 CONCLUSIONS

As related to my original hypotheses:

a) Drainage generally increased NA, g_m and WUE of tamarack and black spruce but did not affect g_s. These results suggest that reduction of non-stomatal limitations to photosynthesis may account for improved ecophysiological performance following drainage.

b) Unexpectedly, urea fertilization decreased NA and g_m of tamarack with the greater N dose having a larger negative effect.

c) As expected, urea fertilization reduced PNUE for both species. However, WUE was unaffected by fertilization.

d) There was no evidence of a trade-off between PNUE and WUE; in fact the two were positively correlated. Maximization of both resource use efficiencies may provide an adaptive advantage under conditions of nutrient deficiency and flooding as found in natural peatlands.

e) PNUE and WUE were generally higher in tamarack than in black spruce at a needle level. Efficient use of nitrogen and water may be an important factor in the survival of the deciduous species, tamarack, under conditions in natural peatlands.

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Chapter 6

EFFECTS OF DRAINAGE AND FERTILIZATION ON SEASONAL PATTERNS OF FOLIAR MASS AND NUTRIENTS OF PEATLAND TAMARACK AND BLACK SPRUCE

6.1 INTRODUCTION

Improved soil conditions accompanying drainage may influence the timing of foliar nutrient accumulation, retranslocation, and resorption, but I am not aware of any study that has evaluated this. In natural minerotrophic peatlands, tamarack showed a rapid decrease in foliar N and P concentration during leaf expansion, and a decrease before needle abscission (Tilton 1977). Tyrrell and Boerner (1987) reported an increase in foliar N and P concentrations during the summer. For black spruce current-year needles, nutrient concentration peaked just after bud break and then decreased until mid summer when concentrations increased again. For older (>one-year-old) needles there was a decrease in spring followed by a slight increase during the summer and a decrease, again, during the winter (Tyrrell and Boerner 1987). While drainage may improve foliar nutrient status it did not raise foliar nutrient levels of tamarack and black spruce to sufficiency levels (chapter 3). Urea fertilization increased foliar N concentration and needle mass of tamarack and black spruce in undrained and drained minerotrophic peatland sites (chapter 3). This suggests that fertilization of drained boreal peatlands in western Canada may be an advantageous management tool.

An understanding of seasonal needle mass and nutrient patterns is essential for designing and timing application of fertilizers to maximize uptake, minimize leaching losses, and to capitalize on internal storage and retranslocation (Nambiar and Bowen 1986) as well as to evaluate foliar responses to such treatments. The effects of drainage and NPK fertilization on foliar mass and nutrients, and gas exchange of tamarack and black spruce have been reported elsewhere (chapters 3, 4 and 5). The goal of the present research was to examine the effect of NPK fertilization of undrained and drained peatlands on: a) seasonal patterns of needle mass and foliar N, P and K concentrations, and b) seasonal foliar nutrient fluxes (rates of movement) of tamarack and black spruce. In chapter 7 I examine the effect of drainage and fertilization of a minerotrophic peatland on needle litter quality for tamarack and black spruce.

6.2 MATERIALS AND METHODS

6.2.1 Study area, field and laboratory procedures

The peatland characteristics, experimental design, and foliar sampling and analysis protocols are presented in detail in chapter 3. The experiment included two drainage treatments (contiguous undrained and drained sites; 75 m apart) and four fertilization treatments: unfertilized (0-0-0 kg.ha^{-1}), N_0PK (0-80-120), N_2PK (200-80-120) and N_4PK (400-80-120). The drained site was ditched in fall 1987. Twelve plots were laid out on each site. Each fertilizer treatment was randomly assigned to three plots at each site and fertilizers were applied on May 28 and 29, 1989. The fertilizer materials were agricultural grade urea, triple superphosphate and KCl.

Foliar samples were taken biweekly from mid-June to mid-October 1989. For tamarack, only short-shoot needles were sampled for analysis. Sampling of tamarack needles was terminated at the end of September following complete yellowing of the needles. For black spruce, current and one- year-old needles were sampled. All foliar and needle litter samples were dried at 65 °C for 24 to 36 h. Needle dry mass was determined from four subsamples of 100 needles per plot. Subsamples of dry needles were ground to pass a 40 mesh sieve for N, P and K analysis. Ground foliar samples were digested and analysed for total N, P and K as described in chapters 2 and 3. For one-year-old needles of black spruce, samples taken on 12 June, 5 July, 30 August and 14 October were analysed in order to provide information at inception and maturation of current needles.

6.2.2 Data analysis

Statistical analyses were carried out on a PC micro-computer using general linear model (GLM) procedures of SAS (SAS Institute Inc. 1987). Data for each species were sorted into two subsets: a) unfertilized and NoPK, and b) N_0PK, N_2PK and N_4PK. Each subset was separately subjected to the following analyses. The homogeneity of error variance was tested by the Shapiro-Wilk procedure (SAS Institute Inc. 1987). In addition, the assumption of compound symmetry (sphericity of the variance-covariance matrix) related to sampling date and its interactions was also tested (Moser *et al.* 1990). For sampling date and its interactions with drainage or fertilization the Huynh-Feldt (H-F) adjustment procedure was used in case of violation of the assumption of compound symmetry. However, this did not change results so it is not presented. The split-plot repeated measures ANOVA procedure (Moser *et al.* 1990) was used to test for seasonal responses of unit needle mass, and foliar N, P and K concentrations to drainage and fertilization. Drainage and fertilization were major factors and sampling date was a sub-factor.

Nutrient fluxes in needles were calculated as follows. Three (tamarack short-shoot needles) and two (black spruce current needles) phases of needle development were identified (Table 6.1; Figs. 6.1, 6.2 and 6.3). For each plot, mean foliar N, P and K fluxes within phases 1 and 3 for tamarack were calculated using equation 1 (Loneragan 1968). There was considerable variability in nutrient patterns within phase 2 for tamarack and both phases for black spruce. For these phases, nutrient fluxes for approximately biweekly sampling periods were calculated using equation 6.1. Weighted (number of days per sampling period) averages for N, P and K fluxes were then calculated for each phase.

$$F = \frac{(Nc2 - Nc1) * (\ln UM2 - \ln UM1)}{(t_2 - t_1) * (UM2 - UM1)} \qquad 6.1$$

where: F - mean nutrient flux (ng nutrient.(ug needle)$^{-1}$.day^{-1}) for each phase

Nc - nutrient content (ng nutrient.needle^{-1}) at time t_1 and t_2 in days

t_1 - start of phase or periodical sampling

t_2 - end of phase or periodical sampling

UM - unit needle mass (ug.needle^{-1}) at times t_1 and t_2

Table 6.1: Phases of needle development defined by needle phenology for short-shoot needles of tamarack and current-year needles of black spruce in response to drainage and fertilization of a minerotrophic peatland at Wolf Creek, central Alberta.

Phase	Calender date - 1989	Needle phenology stage	Duration of phase (days)
	Tamarack short-shoot needles[1]		
1	12 June[2] - 5 July	Elongation	23
2	5 July - 31 Aug.	Maturation	57
3	31 Aug. - 30 Sept.	Before abscission	30
	Black spruce current needles[1]		
1	5 July[2] - 1 Aug.	Elongation	26
2	2 Aug. - 31 Aug.	Maturation	74

[1] Bud break for tamarack was during the third week of May and that of black spruce was during the third and fourth weeks of June;

[2] Indicate the start date which corresponds to first sampling.

Nutrient fluxes within each phase were subjected to ANOVA to test for the effect of drainage and fertilization.

6.3 RESULTS

6.3.1 Seasonal foliar NPK and mass patterns

6.3.1.1 Drainage

Seasonal patterns of foliar N, P and K concentrations and unit needle mass are presented in Fig. 6.1 for tamarack, and in Figs. 6.2 and 6.3 for current- and one-year-old needles of black spruce. The seasonal patterns of foliar N, P and K contents for both species are presented in Appendices 11.13. 11.14 and 11.15. Drainage increased foliar NPK of tamarack. Also foliar NPK and mass of tamarack varied seasonally and drainage altered their seasonal patterns (drainage x date interaction) (Table 6.2; Fig. 6.1).

For current needles of black spruce, drainage increased nutrient concentrations but decreased needle mass (Table 6.3; Fig. 6.2). In contrast to tamarack, only foliar P and mass patterns varied with drainage (drainage x date). For one-year-old needles of black spruce, foliar nutrients varied through the season but needle mass did not, and only N and P concentration were increased by drainage (Table 6.4; Fig. 6.3). As for current needles, only foliar P showed a significant drainage x date interaction.

6.3.1.2 Fertilization and its interaction with drainage

For tamarack, N_0PK fertilization increased foliar P and K concentrations while NPK increased foliar N and needle mass, but decreased P and K (Table 6.2; Fig. 6.1). N_0PK fertilization also significantly affected seasonal patterns of foliar P and K concentrations (Table 6.2), while urea fertilization affected seasonal patterns of foliar N, P and K concentrations and needle mass. In each case there were significant drainage x fertilization and drainage x fertilization x date interactions.

For current-year needles of black spruce, N_0PK and NPK fertilization increased foliar N, P and K concentrations (Table 6.3; Fig. 6.2). There was a significant interaction of drainage with fertlization for P concentration. NPK fertilization significantly influenced seasonal

Figure 6.1: Seasonal response patterns for nitrogen, phosphorus and potassium concentration, and unit needle mass (dry weight basis) for short-shoot needles of undrained and drained tamarack. Mean values ± SE are based on 2 to 3 plots on the undrained site and 4 to 6 subplots on the drained site.

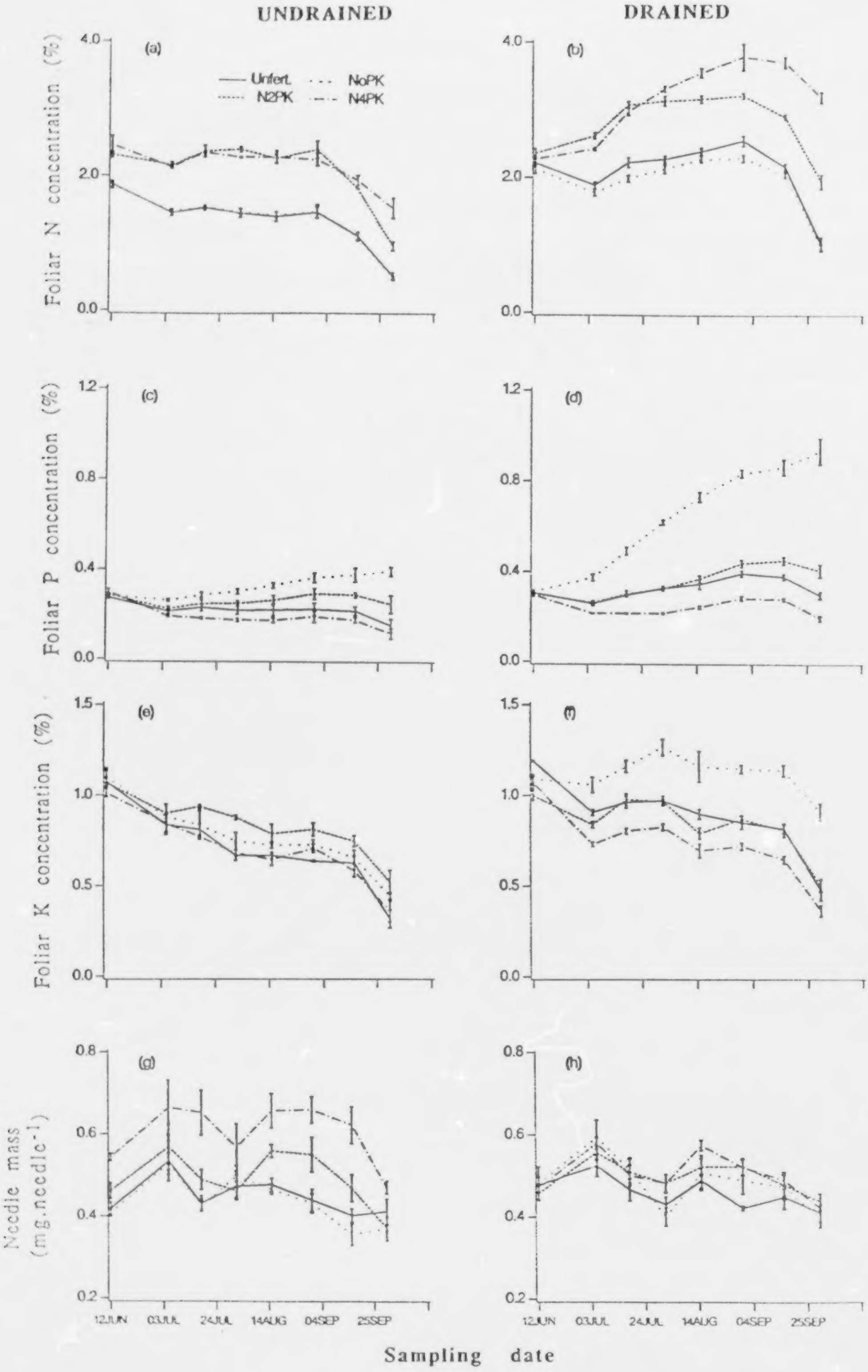
UNDRAINED
DRAINED
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
Unfert.
NoPK
N2PK
N4PK
Foliar N concentration (%)
Foliar P concentration (%)
Foliar K concentration (%)
Needle mass (mg.needle^{-1})
4.0
2.0
0.0
1.2
0.8
0.4
0.0
1.5
1.0
0.5
0.0
0.8
0.6
0.4
0.2
12JUN
03JUL
24JUL
14AUG
04SEP
25SEP
Sampling date

Figure 6.2: Seasonal response patterns for nitrogen, phosphorus and potassium concentration, and unit needle mass (dry weight basis) for current needles of black spruce as in Fig. 6.1.

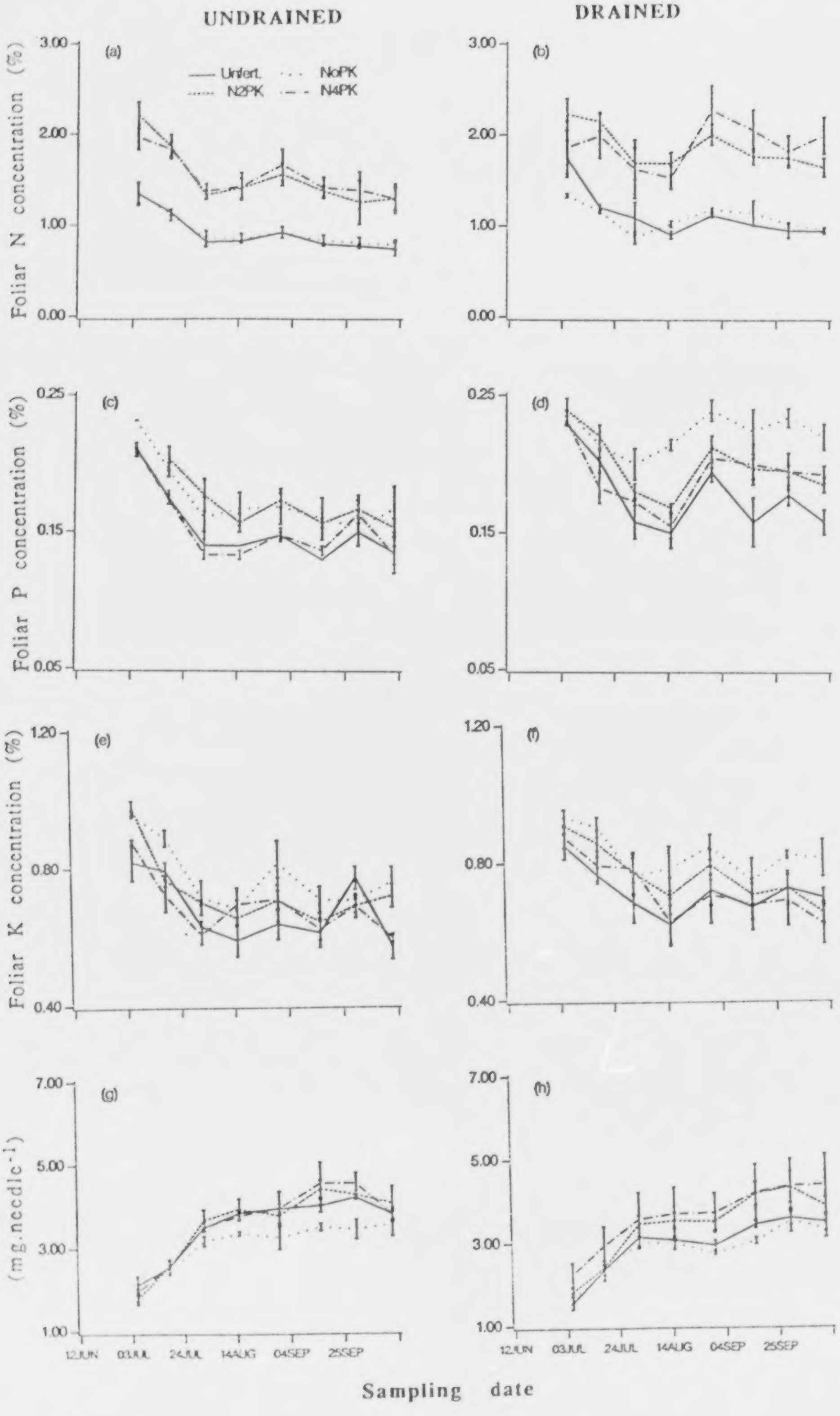
UNDRAINED
DRAINED
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
Unfert.
NoPK
N2PK
N4PK
Foliar N concentration (%)
Foliar P concentration (%)
Foliar K concentration (%)
Needle mass (mg.needle-1)
3.00
2.00
1.00
0.00
0.25
0.15
0.05
1.20
0.80
0.40
7.00
5.00
3.00
1.00
12JUN
03JUL
24JUL
14AUG
04SEP
25SEP
Sampling date

Figure 6.3: Seasonal response patterns for nitrogen, phosphorus and potassium concentration, and unit needle mass (dry weight basis) for one-year-old needles of black spruce as in Fig. 6.1.

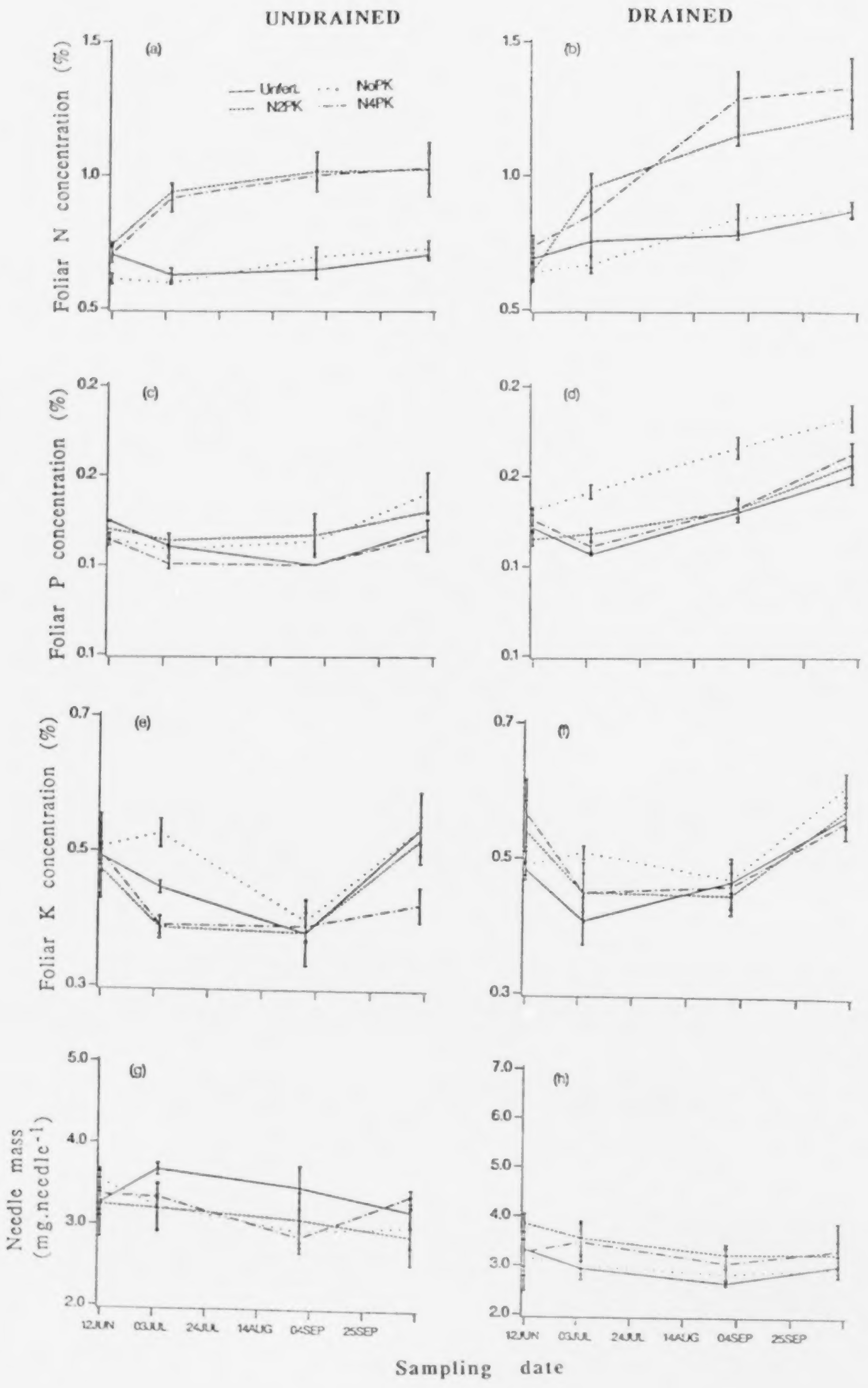
UNDRAINED
DRAINED
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
Unfert.
NoPK
N2PK
N4PK
Foliar N concentration (%)
Foliar P concentration (%)
Foliar K concentration (%)
Needle mass (mg.needle-1)
1.5
1.0
0.5
0.2
0.1
0.7
0.5
0.3
5.0
4.0
3.0
2.0
7.0
6.0
12JUN
03JUL
24JUL
14AUG
04SEP
25SEP
Sampling date

Table 6.2: Summary of ANOVA by repeated measures (P-values) of seasonal foliar nutrient concentration and needle mass responses[1] of tamarack to drainage and N_0PK, N_2PK and N_4PK fertilization of a minerotrophic peatland at Wolf Creek, central Alberta.

Response	Source of variation						
variable	Drain.[2]	Fert.	D x F	Date	D x Date	F x Date	DxFxDate
	[3]Drainage and NoPK fertilization						
N	0.001	0.23	0.18	0.001	0.001	0.36	0.057
P	0.001	0.001	0.002	0.001	0.001	0.001	0.001
K	0.001	0.008	0.016	0.001	0.001	0.001	0.004
Needle mass	0.170	0.79	0.36	0.001	0.001	0.44	0.36
	[4]Drainage and urea fertilization						
N	-[5]	0.001	-	0.001	-	0.001	0.001
P	-	0.001	-	0.001	-	0.001	0.001
K	-	0.001	-	0.001	-	0.001	0.004
Needle mass	-	0.001	-	0.001	-	0.35	0.020

[1] Needle litter not included;

[2] Drain - drainage, Fert - fertilization;

[3] Degrees of freedom for Drain, Fert, D x F, Error 1, Date, D x Date, F x Date, D x F x Date and Error 2 are respectively 1, 1, 1, 8, 7, 7, 7 and 63;

[4] Degrees of freedom for Drain, Fert, D x F, Error 1, Date, D x Date, F x Date, D x F x Date and Error 2 are respectively 1, 2, 2, 12 7, 7, 14, 14 and 94;

[5] Not shown since it involves blanket application of N_0PK.

Table 6.3: Summary of ANOVA by repeated measures (P-values) of seasonal nutrient concentration and needle mass responses[1] of current needles of black spruce to drainage and N_oPK, N_2PK and N_4PK fertilization of a minerotrophic peatland at Wolf Creek, central Alberta.

Response variable	Source of variation						
	Drain.[2]	Fert.	D x F	Date	D x Date	F x Date	DxFxDate
	[3]Drainage and NoPK fertilization						
N	0.024	0.026	0.96	0.001	0.61	0.41	0.15
P	0.001	0.004	0.039	0.001	0.002	0.21	0.14
K	0.022	0.003	0.49	0.001	0.43	0.46	0.56
Needle mass	0.003	0.067	0.24	0.001	0.062	0.43	0.83
	[4]Drainage and urea fertilization						
N	-[5]	0.001	-	0.001	-	0.34	0.93
P	-	0.001	-	0.001	-	0.003	0.20
K	-	0.045	-	0.001	-	0.61	0.49
Needle mass	-	0.12	-	0.001	-	0.032	0.57

[1,2,3,4,5] As in Table 6.2.

Table 6.4: Summary of ANOVA by repeated measures (P-values) of seasonal nutrient concentration and needle mass responses[1] of one-year-old needles of black spruce to drainage and N_0PK, N_2PK and N_4PK fertilization of a minerotrophic peatland at Wolf Creek, central Alberta.

Response variable	Source of variation						
	Drain.[2]	Fert.	D x F	Date	D x Date	F x Date	DxFxDate
	[3]Drainage and NoPK fertilization						
N	0.034	0.58	0.99	0.010	0.16	0.22	0.72
P	0.002	0.013	0.020	0.001	0.001	0.001	0.028
K	0.21	0.11	0.64	0.001	0.10	0.37	0.66
Needle mass	0.29	0.21	0.41	0.051	0.49	0.67	0.25
	[4]Drainage and urea fertilization						
N	-[5]	0.001	-	0.001	-	0.001	0.15
P	-	0.22	-	0.001	-	0.10	0.52
K	-	0.061	-	0.001	-	0.011	0.32
Needle mass	-	0.73	-	0.005	-	0.69	0.53

[1,2,,5] As in Table 6.2.

[3] Degrees of freedom for Drain, Fert, D x F, Error 1, Date, D x Date, F x Date, D x F x Date and Error 2 are respectively 1, 1, 1, 8, 3, 3, 3 and 23;

[4] Degrees of freedom for Drain, Fert, D x F, Error 1, Date, D x Date, F x Date, D x F x Date and Error 2 are respectively 1, 2, 2, 12 3, 3, 6, 6 and 36;

patterns of foliar P concentration and needle mass. For one-year-old needles, NoPK increased foliar P while NPK fertilization increased foliar N (Table 6.4; Fig. 6.3), and there was a significant interaction with drainage in each case. N_0PK fertilization significantly influenced seasonal patterns of foliar P, and the drainage x fertilization x date interaction was significant. NPK fertilization significantly affected seasonal patterns of foliar N, P and K. Seasonal patterns of unit needle mass and foliar N, P and K concentrations are summarized below by species.

Tamarack

Three phases of seasonal foliar N pattern were observed (Fig. 6.1a,b): 1) The needle expansion phase occurred before July 5 (Fig. 6.1g,h). During this phase foliar N concentration in all undrained plots, and in drained-unfertilized and -N_0PK plots decreased (Fig. 6.1a,b). Whereas, in drained-urea fertilized plots foliar N increased (Fig. 6.1b). 2) Needle maturation occurred between July 5 and the end of August. On both undrained and drained sites in unfertilized and N_0PK plots, foliar N concentration remained constant or declined slightly during this period. In drained urea-fertilized plots, foliar N concentration increased throughout this period (Fig. 6.1b). 3) Nitrogen resorption (phase 3) began in late August on both sites, and continued until needle abscission between mid and late September. During this phase foliar N concentration decreased in all fertilization treatments on both sites, but the decline was proportionally less for N fertilized plots (Figs. 6.1a,b).

Foliar P concentration exhibited slightly different seasonal patterns than N (Fig. 6.1c,d). On the undrained site, foliar P concentration in unfertilized and N fertilized plots decreased slightly during phase 1, then remained constant from early July through mid September. In N_0PK plots foliar P concentration increased slightly during phase 2. P declined in all plots except N_0PK plots during phase 3. On the drained site, N_0PK plots showed an increase in foliar P during phase 1, while all plots showed increases during phase 2 (Fig. 6.1d). Foliar P concentration decreased during phase 3 for all except N_0PK plots in which it continued to increase substantially.

On both sites, foliar K concentration decreased during phase 1 regardless of the fertilization treatment (Fig. 6.1e,f). On the undrained site, foliar K continued to decline gradually through phase 2 before a rapid decline during phase 3. On the drained site for all fertilization treatments foliar K concentration decreased rapidly during phase 1, then remained steady or declined gradually before a rapid decrease during phase 3.

The unit needle mass of tamarack on both sites increased during phase 1 due to needle growth (Fig. 6.1g,h). During July (early part of phase two) needle mass decreased slightly for all treatments. In urea plots on the undrained site and in all fertilization treatments on the drained site, needle mass increased during the early part of August. Thereafter needle mass remained constant or decreased gradually before a rapid decrease (except unfertilized and N_0PK plots) during phase 3.

Drainage and urea fertilization altered the onset of senescence of tamarack needles. Needle senescence, as inferred from decrease in needle mass and yellowing, started around early August in undrained-unfertilized and -N_0PK plots, and near the end of August in urea fertilized plots. On the drained site decline in unit needle mass began around mid August, while yellowing of needle tips began around mid September in all plots. Needles had completely yellowed by the end of September in all plots on both sites.

Black spruce

Two phases of seasonal foliar N pattern were observed for current needles of black spruce (Fig. 6.2a,b): 1) The needle expansion phase continued until late July. Foliar N concentration in current needles of black spruce in all plots decreased during this period. 2) The needle maturation phase occurred from late July through mid October. During this period foliar N remained constant or increased slightly. On the drained site, foliar N trends were similar to those on the undrained site, except that during the second phase foliar N increased in urea-plots and foliar P increased in N_0PK-plots.

Foliar P concentration in current needles of black spruce on the undrained site exhibited similar seasonal patterns to those of foliar N: a decrease during needle expansion phase and relatively constant for the remainder of the season (Fig. 6.2c). On the drained site, a decrease in foliar P during phase 1 was followed by an increase after mid August (Fig. 6.2d) then was steady through mid October. On both sites, foliar K concentration of current needles decreased during the needle expansion phase regardless of the fertilization treatments (Fig. 6.2e,f). This was followed by steady levels during the rest of the season.

Black spruce bud break occurred after the second week of June and was completed on both sites by the first week of July. The mass of current-year needles in undrained and drained sites increased rapidly during phase one regardless of the fertilization treatment (Fig. 6.2g,h). Then needle mass remained relatively constant until September when it increased slightly for all fertilization treatments on the drained site and N-fertilized plots on the undrained site. Maximum needle mass was reached after the second week of September on the undrained site and around late September on the drained site. Needle masses were similar for all treatments by mid October. Needle mass for N_0PK was consistently lowest after mid-July with the difference to the next lowest treatment (unfertilized) being greater for the undrained site (Fig. 6.2g,h). With drainage, N fertilization significantly increased unit needle mass after early August.

For one-year-old needles of black spruce, foliar N was steady except for N-fertilized plots it increased throughout the season on the drained site, while that on the undrained site increased during phase 1 and then remained constant (Fig. 6.3a,b). In all drained plots, foliar P increased gradually after July 5 with the earliest and highest increase with N_0PK and N_2PK fertilization (Fig. 6.3d). On both sites, there was a general decrease in K to early July, remaining steady to late August then followed by an increase (Fig. 6.3e,f).

6.3.2 Fluxes of N, P and K in needles

Fluxes of foliar nutrients calculated by equation 1 assume a linear relationship between mineral nutrient content and unit needle mass. Although this assumption was not met, fluxes assist in comparing the pattern of nutrient movement between phases (Fife and Nambiar 1982) as affected by tree species, drainage and fertilization.

For tamarack, drainage without fertilization increased rates of efflux (negative value) of P and K during phase 1 and of influx of N, P and K during phase 2 (Table 6.5). Influx of nutrients is defined here as the rate of nutrient accumulation per unit needle mass, and vice versa for efflux of nutrients. During phase 2, influxes of N and P were generally

Table 6.5: Nutrient fluxes in current foliage and ANOVA results for foliar N, P and K fluxes of tamarack and black spruce during phases of needle development in response to drainage and fertilization of a minerotrophic peatland at Wolf Creek, central Alberta.

Foliar	Foliar nutrient fluxes								Analysis of variance					
response	Undrained site				Drained site				Drainage & N_0PK Fert.[2]			Drainage& Urea Fert.		
variable	Unfert.	N_0PK	N_2PK	N_4PK	Unfert.	N_0PK	N_2PK	N_4PK	Drain.	Fert.	D*F	Drain.	Fert.	D*F
						Tamarack								
N phase 1[1]	-0.008	0.028	0.128	0.500	-0.058	0.023	0.325	0.277	0.55[3]	0.47	0.72	-[4,5]	0.06	0.80
phase 2	-0.123	-0.130	0.067	0.053	0.086	0.059	0.184	0.515	<0.001	0.95	0.90	-	0.004	0.07
phase 3	-0.437	-0.493	-0.910	-0.590	-0.688	-0.728	-0.747	-0.655	0.10	0.28	0.79	-	0.001	0.03
P phase 1	-0.002	0.020	-0.004	-0.027	-0.010	0.058	0.009	-0.014	<0.001	<0.001	<0.001	-	<0.001	<0.001
phase 2	-0.006	0.007	0.010	<0.0001	0.012	0.069	0.028	0.007	<0.001	0.003	<0.001	-	<0.001	<0.001
phase 3	-0.033	-0.013	-0.067	-0.057	-0.048	-0.037	-0.046	-0.062	0.95	0.73	0.64	-	0.85	0.96
K phase 1	-0.005	0.014	0.017	0.002	-0.083	0.088	0.008	-0.069	0.03	0.02	0.008	-	0.35	0.14
phase 2	-0.062	-0.056	-0.023	-0.027	-0.044	-0.024	-0.005	-0.015	0.13	0.40	0.68	-	0.17	0.75
phase 3	-0.153	-0.160	-0.243	-0.230	-0.173	-0.198	-0.213	-0.207	0.86	0.94	0.98	-	0.02	0.64
						Black spruce								
N phase 1	0.005	-0.005	0.156	0.155	0.132	0.075	0.273	0.185	0.34	0.75	0.82	-	0.19	0.89
phase 2	0.001	0.001	0.020	0.011	-0.012	0.032	0.030	0.100	0.68	0.32	0.33	-	0.21	0.20
P phase 1	-0.003	-0.001	0.025	0.008	0.018	0.026	0.024	0.012	0.005	0.42	0.56	-	0.06	0.08
phase 2	0.001	0.003	-0.001	0.001	0.003	0.007	0.004	0.009	0.28	0.30	0.72	-	0.29	0.75
K phase 1	0.069	0.059	0.111	0.055	0.144	0.132	0.145	0.105	0.005	0.57	0.95	-	0.28	0.83
phase 2	0.011	0.016	0.010	0.005	0.001	0.020	-0.004	-0.002	0.76	0.43	0.82	-	0.32	0.74

[1] As defined in Table 6.1

[2,3,4,5] As described in Table 6.2.

higher on the drained than on the undrained site. N_0PK fertilization increased (Table 6.5) influx of P during phases 1 and 2, with drainage resulting in greater increases. NPK fertilization increased (Table 6.5) influx of N and P during phase 2 even though it resulted in significant ($P<0.001$) efflux of P (on the undrained site) during phase 1. During phase 3, rates of resorption of N and K on the undrained site were generally higher in NPK-treated than in N_0PK plots. To the contrary, the rate of resorption of P on either site was not affected by NPK fertilization.

For black spruce, drainage without fertilization resulted in an efflux of P and influx of K during phase 1 (Table 6.5). N_0PK had no effect on fluxes of N, P and K in either phase. N-fertilization increased influx of P on the undrained site during phase 1.

6.4 DISCUSSION

At my study area, drainage delayed bud break and senescence of needles, increased foliar nutrients (late August) for tamarack and black spruce, but decreased unit needle mass of the later species (chapter 3). N_0PK increased foliar P and K concentrations of both species. On the other hand, urea fertilization increased N concentration, but decreased P and K, probably as a result of dilution associated with increased needle mass. Urea fertilization delayed needle senescence on the undrained site. The present study shows that drainage and fertilization also affected seasonal dynamics of foliar nutrients and needle mass.

6.4.1 Foliar NPK patterns

Seasonal patterns of foliar N, P and K concentrations generally resemble those reported for tamarack from natural peatlands (Tilton 1977, 1978; Tyrrell and Boerner 1987) and for upland deciduous species (Guha and Mitchell 1966; Ponder and Phares 1979; Elowson and Rytter 1988). Seasonal foliar nutrient patterns similar to those I found in black spruce have been reported for black spruce and other evergreen temperate conifers (Lowry and Avard 1969; Katainen and Valtonen 1985; Tyrrell and Boerner 1987). In all these reports, (except Katainen and Valtonen 1985) foliar nutrient dynamics have not been expressed in terms of nutrient content (mass of element per needle); hence, no definite statements can be made about retranslocation.

The timing of different phases on nutrient accumulation and retranslocation is a function of the growth cycle of the tree (Fife and Nambiar 1982, 1984; Katainen and Valtonen 1985) which in turn is partly influenced by environmental conditions. Silvicultural treatments that increase availability and uptake of nutrients seem to result in changes of foliar nutrient status and timing of nutrient accumulation and retranslocation. In this study, ditch drainage and NPK fertilization changed seasonal nutrient patterns, status and fluxes.

N content did not change during phase 1 for both tree species (results not presented). This suggests that the decrease in foliar N concentration during needle expansion is the result of N dilution due to greater relative accumulation of carbohydrates and other cellular materials (Woodwell 1974). On the other hand, declining P and K content of one-year-old needles of black spruce in some plots during phase 1 likely indicates retranslocation of these nutrients to current needles.

A decrease of P (undrained-N_4PK plots) and K (drained-unfertilized and N_4PK plots) in young needles of short-shoots of tamarack, and of P (undrained-unfertilized plots) in current needles of black spruce during phase 1 was unexpected. This may reflect the relatively greater mobility of P and K compared to N (Fife and Nambiar 1982), inadequate availability of P and K, and development of new sinks within trees. Nutrient retranslocation from young needles is strongly influenced by formation of new sinks within the tree (Fife and Nambiar 1984). Indeed, withdrawal of P and K occurred during the period of long-shoot elongation (i.e., between mid-June and late-July) for tamarack. I am not aware of the cause of withdrawal of P from young needles of unfertilized black spruce.

In general, drainage increased seasonal foliar nutrient concentration of both species indicating an increase in nutrient availability and uptake attributed to improved soil conditions (chapter 3). Fertilization increased seasonal foliar N, P and K concentrations, contents and fluxes in tamarack and black spruce during phase 2 probably due to increased availability and uptake, and retranslocation from older tissues due to increased strength of new sinks resulting from fast growth (Fife and Nambiar 1982). However, there was no decrease in N, P and K content of one-year-old needles of black spruce for all fertilization treatments suggesting no retranslocation of nutrients from one-year-old needles during the summer (phase 2). These results are consistent with those of *Pinus sylvestris* in Finland (Katainen and Valtonen 1985), but are contrary to those reported for *Pinus radiata* in Australia (Fife and Nambiar 1982, 1984).

On undrained-unfertilized plots there was little change in foliar N, P and K concentration during phase 2 probably due to low nutrient availability. Fertilization of these plots resulted in less seasonal increases in foliar N, P and K concentrations as compared to drained plots. Thus nutrient availability was probably not the sole cause of low foliar nutrient concentrations on the undrained site. Nutrient uptake on the undrained site may have been restricted by shallow and low rooting volume (Lieffers and Rothwell 1987), low soil temperature (Whitefield and Smika 1979; Uresk *et al.* 1979; Running and Reid 1980; DeLucia 1986; van Cleve *et al.* 1990) and poor soil aeration, all related to a high water table (chapter 3). Restricted soil aeration may reduce transport of N and P from roots to leaves (Shaprio *et al.* 1956; Smith *et al.* 1989) as a result of reduced transpiration.

6.4.2 Needle mass patterns

6.4.2.1 Tamarack

Seasonal changes in short-shoot needle mass of tamarack followed the same trends as deciduous temperate trees (Clausen and Kozlowski 1967; James and Smith 1978; Tyrrell and Boerner 1987; Gower *et al.* 1989). Bud break occurred by mid May, and expansion of short-shoot needles was completed around late June. These phenological results corroborate other studies on tamarack (Tilton 1977; Clausen and Kozlowski 1967). Following this, unit needle mass decreased until late July and then was steady or declined slowly for the rest of the season. The mid-summer decline may be related to translocation of carbohydrates and other cellular materials to actively growing tissues (roots, stemwood, branchwood and long-shoots).

These results are both consistent (Clausen and Kozlowski 1967) and contrary (Tilton 1977) with those for tamarack in Minnesota. My results of increased unit needle mass on drained unfertilized plots during the first half of August agree with those of tamarack in undrained peatland (Tilton 1977).

My study showed that drainage had no net effect on seasonal needle mass although it varied during the season. Nitrogen fertilization resulted in an increase in needle mass in mid-summer and this response was more pronounced on the undrained site. I hypothesize that, owing to the initially low root:shoot ratio of tamarack in natural peatlands and a thicker and more aerated soil profile on the drained site, development of an extensive root system in recently drained peatlands may be important for uptake of more water and nutrients. This would involve a preferential allocation of carbon to belowground components (chapter 3). On the other hand, the belowground carbon sink strength of trees on the undrained site is small. Thus, increased unit needle mass in N fertilized plots on the undrained site may be related to preferential allocation of carbon to aboveground components, including foliage, as a response to improved nutritional status. Further research is required on the effect of N fertilization on carbon allocation in undrained and drained peatlands.

Needle senescence is governed genetically, by photoperiod and by nutrient availability, especially N concentration in needles (Thomas and Stoddart 1980). In my study, N fertilization delayed the start of loss in unit needle mass in tamarack on the undrained site for 2 weeks. This may be related to increased foliar N on the undrained N fertilized plots.

6.4.2.2 Black spruce

Seasonal patterns of needle mass of black spruce followed those found in other evergreen temperate trees (Wells 1965; Lowry and Avard 1969; Katainen and Voltanen 1985). In contrast to tamarack, bud break in black spruce occurred later during the second and third weeks of June. This was followed by a rapid increase in mass of current needles of black spruce during July, a trend observed in other temperate evergreen gymnosperms (Lowry and Avard 1969; Tilton 1977; Katainen and Voltanen 1985). I found that unit mass of current needles remained constant during

August. During this period photosynthate was likely being allocated to stem growth (Gordon and Larson 1968; Dickman and Kozlowski 1968; Glerum and Balatinecz 1980).

In contrast to tamarack, drainage without fertilization caused a decrease in mass of current needles of black spruce from mid August to mid October. This may be related to higher shoot-root biomass ratio of black spruce as compared to tamarack. In chapters 2 and 3 I hypothesized that restricted N supply and initially unfavourable shoot/root ratio of recently-drained peatland black spruce may result in preferential allocation of a higher proportion of photosynthate to belowground than aboveground components.

N_0PK fertilization decreased the mass of current needles on the undrained site from mid July to late September. A corresponding decrease in needle mass of current needles on the drained site occurred beween late August and early September. Although I did not check for visual symptoms, this decrease in needle mass may be related to Cu and Mn deficiencies induced by application of P fertilizer (see table 4.3). Phosphate fertilizers are known to induce micronutrient deficiencies, especially Zn and Cu, in plants growing in mineral soils (Olsen 1972; van Lear and Smith 1972; Payne *et al.* 1986).

N fertilization increased mass of current needles from mid August to late September on the drained site. However, unit needle mass of black spruce was greater in undrained- as compared to drained-N-fertilized plots. This was probably due to increased allocation of photosynthate to foliage growth of N-fertilized trees since there likely was no change in the strength of the belowground sink in urea fertilized natural peatland as discussed previously.

6.5 CONCLUSIONS

In general drainage and fertilization changed phenology of needles, seasonal foliar nutrient patterns and status, and fluxes. However, it appears that the timing of different phases of foliar nutrient retranslocation and fluxes depends largely on the growth which is genetically and environmentally controlled. Drainage (alone) delayed bud break in spring (both species) and needle senescence (tamarack). On the other hand, urea-fertilization (alone) delayed loss in unit needle mass on the undrained site.

Silvicultural treatments that increase nutrient availability and uptake may modify the direction and magnitude of foliar nutrient retranslocation and fluxes. For example, P and K retranslocated from young needles presumably in response to rapid growth of long-shoots of unfertilized tamarack in late spring, with greater effluxes on the drained site. On the other hand, there was net accumulation of N in needles of urea plots, and P in N_0PK plots during the summer for both species, with greater accumulation on the drained site.

Retranslocation of nutrients presumably from older ($\geq$1 yr) to current needles of unfertilized black spruce occurred only in late spring. As a consequence photosynthesis of older needles may be reduced due to lowered nutrient concentrations. Increased nutrient availability through fertilization in early spring could result in early uptake of nutrients and minimize the observed retranslocation and hence maintain higher rates of photosynthesis in older needles.

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Chapter 7

NEEDLE LITTER RESPONSES OF PEATLAND TAMARACK AND BLACK SPRUCE TO DRAINAGE AND FERTILIZATION

7.1 INTRODUCTION

Tamarack (*Larix laricina* (Du Roi) K. Koch.) and black spruce (*Picea mariana* (Mill.) B.S.P.) are predominant tree species in peatlands in North America (Bares and Wali 1979). Black spruce has adapted to the cold soil temperature, poor soil aeration and low nutrient supply of peatlands through: a) low nutrient requirements; b) efficient resorption of nutrients before needle abscission (Hom and Oechel 1983; Tyrrell and Boerner 1987); and c) long-term retention of photosynthetically-active needles which increases the carbon return per unit of invested nutrient (Small 1972). Unlike black spruce, tamarack is a deciduous conifer. The persistence of tamarack in nutrient-poor peatlands might be linked to its ability for nutrient conservation (Small 1972; Tilton 1977; Chapin and Kedrowski 1983; Tyrrell and Boerner 1987).

Drainage of peatlands in central Alberta improved foliar nutrient status of tamarack and black spruce (Lieffers and Macdonald 1990; chapters 2, 3 and 6), but did not seem to alleviate sub-optimal foliar nutrient concentrations that existed before ditching. NPK fertilization significantly increased foliar nutrient concentrations and may have resulted in sufficiency levels for both species. Drainage and fertilization may also modify foliar nutrient resorption. I hypothesize that an increase in nutrient availability and uptake reduces nutrient resorption resulting in increased nutrient concentration and content (mass of element per needle) of needle litter, an indication of reduced nutrient use efficiency. I also hypothesize that this effect may be greater in the short term, for tamarack than for black spruce. This is because the ditching and fertilization treatments are not expected to have significant effects in old needles (which form black spruce needle litter) that developed before application of the treatments. In this paper nutrient use efficiency encompasses the following dependent variables: a) nutrient mass (both relative and absolute) returned to the forest floor by needle litterfall; b) resorption of nutrient before needle abscission; and c) needle litter mass per unit of nutrient.

In chapter 6 I evaluated the effect of drainage and NPK fertilization on seasonal patterns of needle mass and foliar nutrients for tamarack and black spruce. The goal here is to examine the effect of NPK fertilization of undrained and drained peatlands on: a) needle litter N, P and K concentrations and contents; and b) the degree of resorption of N, P and K before abscission of needles in tamarack and black spruce.

7.2 MATERIALS AND METHODS

7.2.1 Study area and experimental design

The peatland characteristics (soil and plant community) and experimental design are documented in chapter 3. The experiment included two drainage treatments (contiguous undrained and drained sites; 75 m apart) and four fertilization treatments, i.e., unfertilized (at doses of 0-0-0 kg.ha^{-1}), N_0PK (0-80-120), N_2PK (200-80-120 and N_4PK (400-80-120). The drained site was ditched in Fall 1987. Twelve plots were laid out at each of undrained and drained sites. The four fertilizer treatments were randomly assigned to the 12 plots on the drained site. Fertilization levels were assigned to undrained plots such that control plots (unfertilized and N_0PK) were on an upslope position relative to the N dosage plots in order to minimize lateral contamination by N ions of control plots. Fertilizers composed of urea, triple superphosphate and KCl were applied on 28 and 29 May 1989.

7.2.2 Needle litter sampling and analysis

Needle litter of black spruce was sampled on 17 September and that of tamarack on 30 September 1989 by spreading a nylon cloth on the forest floor under trees selected for foliar sampling in each plot on each site and shaking the trees, followed by hand separation from other litter materials. Drying, weighing and digestion of needle litter samples and analysis for N, P and K were as described in chapter 2.

7.2.3 Data analysis

Needle litter mass per unit nutrient (NMU) was calculated as the inverse of nutrient concentration in the needle litter (Vitousek 1982). Nutrient resorption before abscission was calculated only for tamarack needle litter using equation 7.1 (Gower *et al.* 1989). Nutrient resorption for black spruce was not estimated since 1989 seasonal maximum nutrient concentration for older (>2 year-old) needles was not determined. Calculation of NMU and resorption assume no loss of cellular materials, especially carbon, during senescence of needles. To the contrary, in this study there was a decrease in needle mass attributable to resorption of cellular materials (chapter 6). However, nutrient concentration of needle litter of either species was not corrected to take into account loss in cellular materials during senescence of needles. This is because maximum needle mass of foliage from which needle litter of black spruce formed was not measured.

$$R\% = \frac{(SNM - NLc) * 100}{SNM} \qquad 7.1$$

where: R% - nutrient resorption (%) for tamarack

SNM - 1989 seasonal maximum nutrient concentration (% dry wt.) after full expansion (maximum unit needle mass) of the needles (chapter 6)

NLc - needle litter nutrient concentration (%)

Statistical analyses were carried out using SAS-PC (SAS Inst. Inc. 1987). Data for each species were sorted into two subsets according to the following grouping of fertilizer treatments: a) unfertilized and NoPK, and b) N_0PK, N_2PK and N_4PK. The second grouping was to isolate the effect of N fertilization from that of N_0PK. Prior to the analysis of variance (ANOVA), the null hypothesis for homogeneity of variance for each error term was tested by the Shapiro-Wilk procedure (SAS Inst. Inc. 1987). Nutrient resorption data were subjected to arcsine transformation because they were percentages (Sokal and Rohlf 1969) since the error variance was heterogenous. The ANOVA model tested for the effects of drainage, fertilization and their interactions.

7.3 RESULTS

Significant effects of drainage and fertilization were found for needle litter nutrient concentration and content for both species. For tamarack, drainage resulted in a significant increase in N and P concentration and content, but decreased K concentration and content of needle litter (Table 7.1; Figs. 7.1 and 7.2). For black spruce, corresponding increases occurred for N concentration and content, but there was no effect on P or K. Drainage had no significant effect on unit needle mass of tamarack or black spruce.

For tamarack, N_0PK fertilization significantly increased P and K concentrations and contents of needle litter, and this effect was more pronounced on the drained site (Table 7.1; Figs. 7.1 and 7.2) . N_0PK fertilization did not affect black spruce needle litter nutrient concentration nor did it affect unit needle mass of tamarack or black spruce.

N fertilization significantly increased N concentration and content, and this effect was more pronounced on the drained site. However, N fertilization decreased P and K concentrations and contents of needle litter of tamarack, with a greater decrease resulting from N_4PK addition (Table 7.1). The decrease in P was greater on the undrained relative to the drained site. For black spruce, N fertilization significantly increased N concentration of needle litter (Table 7.1). The unit needle litter mass of tamarack was increased by N fertilization,

Table 7.1: Summary of ANOVA (P-value) for needle litter nitrogen, phosphorus and potassium concentrations and contents for tamarack and black spruce in response to drainage and fertilization of a minerotrophic peatland at Wolf Creek, central Alberta.

		Tamarack		B. spruce		Tamarack		B. spruce	
		Concn.	Cont.	Concn.	Cont.	Concn.	Cont.	Concn.	Cont.
		Drainage and NoPK fertiliz.[1]				Drainage and urea fertiliz.[2]			
N	Drain.[3]	<0.001	<0.001	0.017	0.020	-[4]	-	-	-
	Fert.	0.14	0.16	0.55	0.80	<0.001	<0.001	0.046	0.079
	D x F	0.78	0.73	0.68	0.42	<0.001	<0.001	0.40	0.77
P	D	<0.001	<0.001	0.18	0.081	-	-	-	-
	F	<0.001	<0.001	0.14	0.16	<0.001	<0.001	0.62	0.89
	D x F	<0.001	0.001	0.84	0.58	<0.001	<0.001	0.61	0.41
K	D	<0.001	<0.001	0.14	0.094	-	-	-	-
	F	<0.001	<0.001	0.93	0.96	<0.001	<0.001	0.96	0.95
	D x F	<0.001	<0.001	0.26	0.22	<0.001	<0.001	0.42	0.29

[1] Degrees of freedom for Drain., Fert. D x F and Error were 1, 1, 1, and 8

[2] Degrees of freedom for Drain., Fert. D x F and Error were 1, 2, 2, and 12, respectively;

[3] Drain - drainage, Fert. Fertilization;

[4] Not shown since it involves blanket application of N_oPK.

with N_4PK resulting in the greatest increase (Fig. 7.3). Needle litter mass of black spruce was not affected by N fertilization.

For tamarack, drainage had no effect (Table 7.2; Fig. 7.4) on resorption of N but decreased resorption of P, and increased that of K in needle litter. N_oPK fertilization significantly (Table 7.2, Fig. 7.4) decreased resorption of P and K, and this effect was more pronounced on the drained than on the undrained site. Similarly, N fertilization decreased resorption of N with a greater decrease resulting from N_4P K

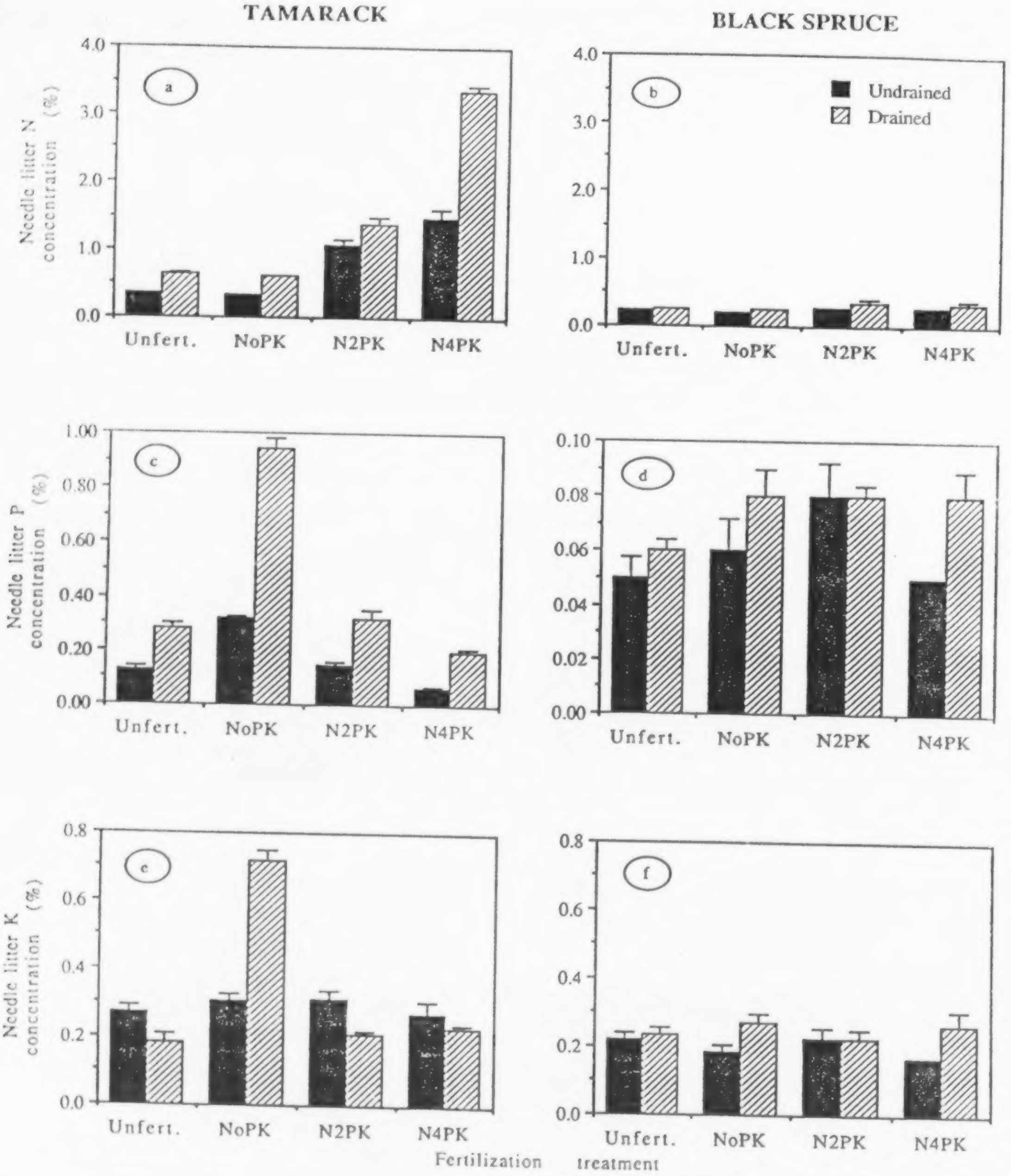

Figure 7.1: Needle litter nutrient concentration of tamarack and black spruce in response to drainage and NPK fertilization of a minerotrophic peatland at Wolf Creek, central Alberta.

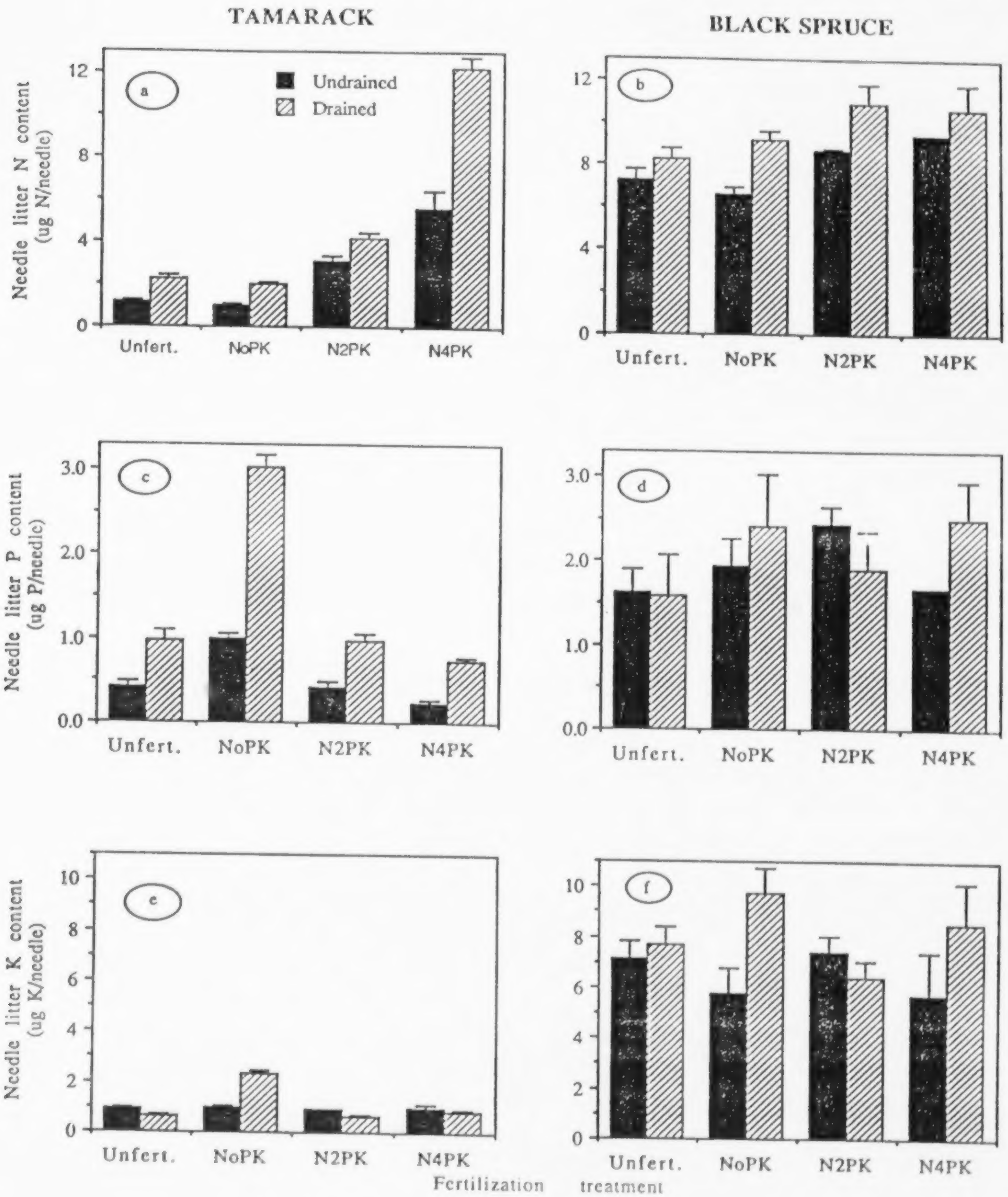

Figure 7.2: Needle litter nutrient content of tamarack and black spruce in response to drainage and NPK fertilization of a minerotrophic peatland at Wolf Creek, central Alberta.

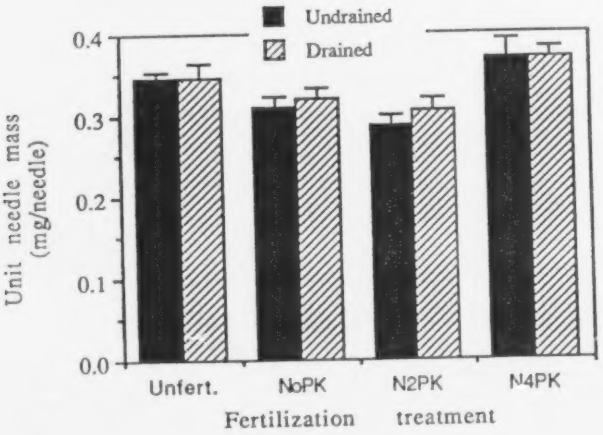

Figure 7.3: Unit needle litter mass of tamarack in response to drainage and NPK fertilization of a minerotrophic peatland at Wolf Creek, central Alberta.

Table 7.2: Probability values from ANOVA of nutrient resorption for tamarack in response to drainage and fertilization of a minerotrophic peatland at Wolf Creek, central Alberta.

	Foliar nutrient					
	N	P	K	N	P	K
	Drainage and NoPK fert.[1]			Drainage and urea fert.[2]		
Drain.[3]	0.16	0.002	0.007	-[4]	-	-
Fert.	0.85	<0.001	0.009	<0.001	<0.001	0.01
D x F	0.26	0.28	0.007	0.17	0.08	0.04

[1,2,3,4]As defined in Table 7.1

Table 7.3: Probability values from ANOVA of needle mass per unit mass of nitrogen (N), phosphorus (P) and potasium (K) of needle litter of tamarack and black spruce near the end of the first growing season following fertilization of undrained and drained minerotrophic peatland sites at Wolf Creek, central Alberta.

		Needle mass per unit of nutrient mass					
		N	P	K	N	P	K
		Drainage and NoPK fert.[1]			Drainage and urea fert.[1]		
Tamarack							
	Drain[3]	<0.001	0.003	0.005	-[4]	-	-
	Fert	0.14	0.001	0.002	<0.001	<0.001	<0.001
	D x F	0.47	0.14	0.006	<0.001	<0.001	0.002
B. spruce							
	D	0.013	0.14	0.13	-	-	-
	F	0.52	0.22	0.68	0.009	0.50	0.82
	D x F	0.60	0.95	0.19	0.50	0.60	0.30

[1,2,3,4]As in Table 7.1.

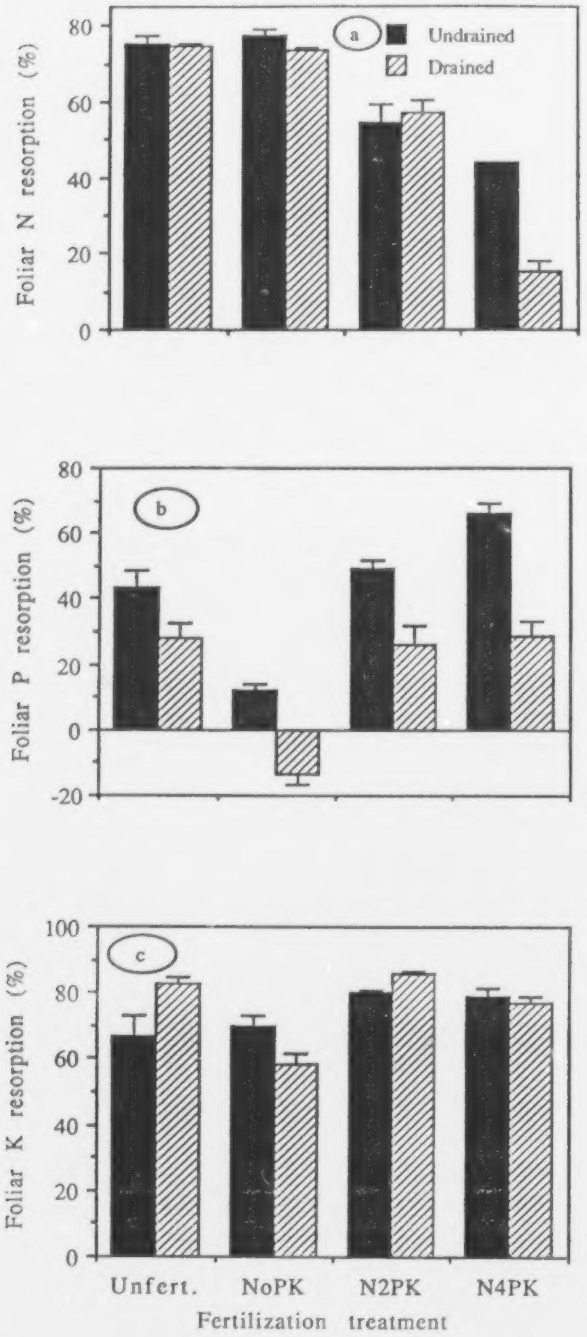

Figure 7.4: Foliar N, P and K resorption before abscission of needles of tamarack in response to drainage and NPK fertilization of a minerotrophic peatland at Wolf Creek, central Alberta.

on the drained site. However, N fertilization increased resorption of P and K.

Drainage decreased (Table 7.3; Fig. 7.5) NMU of N and P of tamarack, and N of black spruce. To the contrary, drainage increased NMU of K in tamarack, but had no effect on P and K of black spruce. N_0PK fertilization did not affect N-NMU but decreased (Table 7.3; Fig. 7.5) P- and K-NMUs of tamarack and for K the decrease was freater on the drained than on the undrained site. N_0PK fertilization did not significantly influence needle litter mass per unit nutrient (N-NMU) of tamarack, and N-, P- and K-NMU of needle litter of black spruce.

As expected, N fertilization decreased (Table 7.3; Fig. 7.5) N-NMU for both tree species. However, N fertilization resulted in a concomitant increase in P- and K-NMU of needle litter of tamarack with a greater increase of P on the undrained site and that for K on the drained site. P- and K-NMU of black spruce were not affected by N fertilization.

7.4 DISCUSSION

7.4.1 N, P and K concentration and content, and needle mass

Drainage increased N of needle litter of tamarack and black spruce. This may reflect the initially high foliar N (chapter 6) as well as decreased resorption. To the contrary, drainage decreased K of needle litter of tamarack although foliar K increased (chapter 3). This may be related to both increased resorption and leaching prior to needle abscission. Drainage delayed senescence of needles of tamarack (chapters 3 and 6). This may have provided more time for leaching of K since it is very mobile (Waring and Schlesinger 1985). Increased foliar N, on the drained site, could also have enhanced leaching of K (Miller *et al.* 1976).

The lack of a significant effect of drainage on unit needle litter mass of both species suggests that drainage had no effect on structural material of needle litter. The structural materials of conifers cannot be

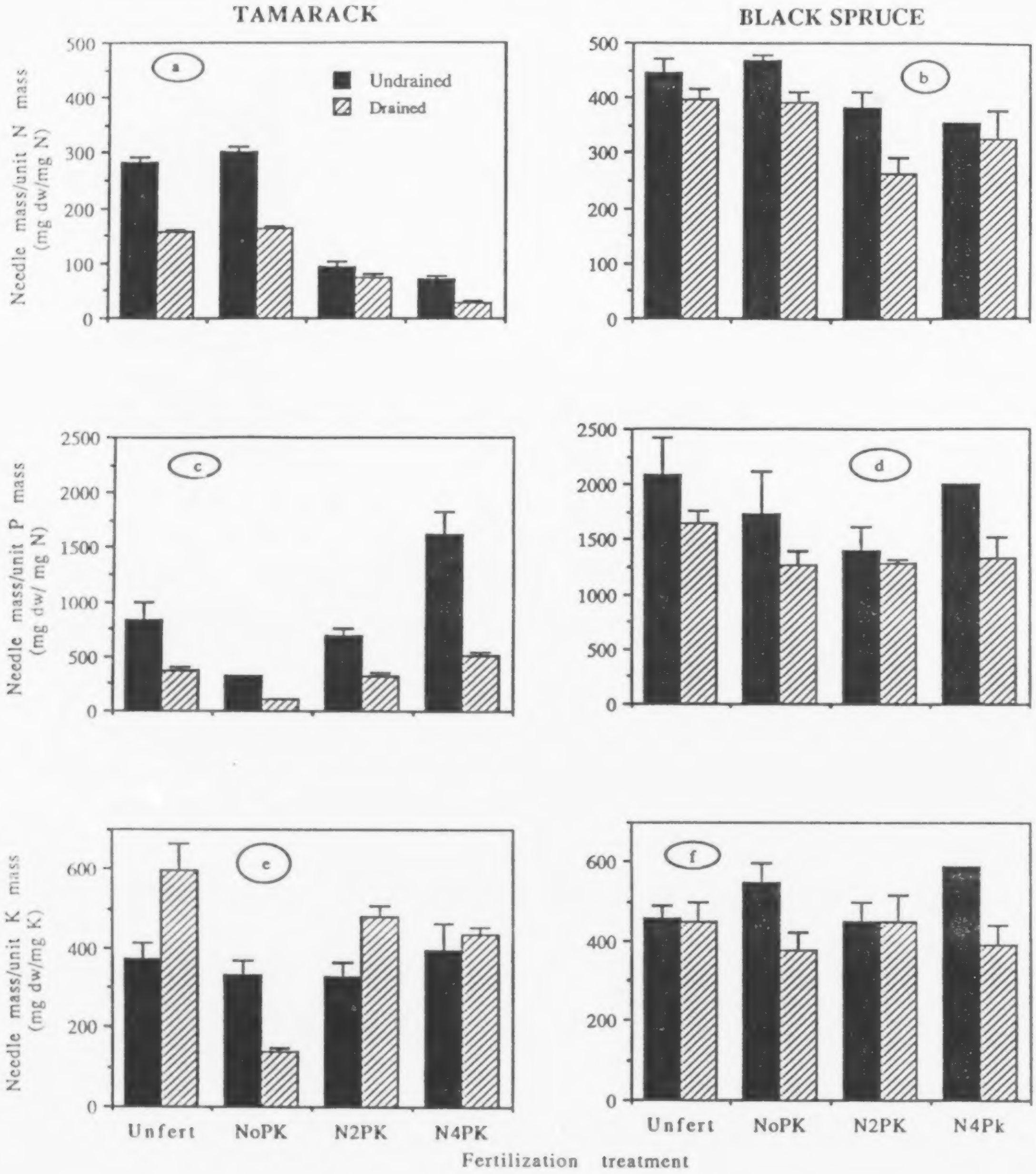

Figure 7.5: Needle litter mass per unit of nutrient mass for tamarack and black spruce in response to drainage and NPK fertilization of a minerotrophic peatland at Wolf Creek, central Alberta.

hydrolysed and used for other purposes (Margolis and Brand 1990). For black spruce, needle litter originated from foliage that formed many years before ditching, and allocation of carbon for structural function of these needles was not expected. Because the unit needle mass of foliage (chapter 3) and of litter for tamarack were not affected by drainage, it is likely that the ratio of structural to hydrolysable materials was similar for trees on the undrained and drained sites.

N_0PK fertilization increased needle litter P of tamarack but did not affect needle litter P of black spruce. Increased needle litter P with N_0PK fertilization has been reported for *Pinus elliottii* on lateritic podzolic soil (Maggs 1985) and *Betula pubescens* on a drained bog (Paavilainen 1987). However, Paavilainen (1987) observed that N_0PK had no effect on needle litter P of *Pinus sylvestris* on a drained bog (Paavilainen 1987). In plants, nutrients are preferentially allocated to more metabolically active tissues. In my study, needle litter of black spruce originated from old (>8-year-old) foliage. Subsequently, very little fertilizer P and K may have been allocated to this foliage.

Combined NPK fertilization increased N in tamarack and black spruce needle litter. This agrees with results for other species (Miller *et. al.* 1976; Paavilainen 1987) and for black spruce (Mahendrappa and Weetman 1973; Mahendrappa and Salonius 1982). This increase in needle litter N may be related to increased N uptake and reduced resorption. NPK fertilization decreased P and K concentration of needle litter of tamarack. This may be due to increased resorption since P and K contents of needle litter of tamarack decreased with N_4PK fertilization.

Increased unit needle litter mass of N_4PK-fertilized tamarack is likely due to initially high unit needle mass. This suggests that high N dosage may result in accumulation of more structural materials in foliage. This reasoning is based on the assumption that structural materials of needles could not be utilized for other purposes (Margolis and Brand 1990) and that there was complete resorption of proteins and other cellular materials before needle abscission.

Drainage and N fertilization separately or together increased the amount of nutrients (in a unit mass of needle litter) returned to the forest floor (Figs. 7.1 and 7.2). These results are consistent with those of

N-fertilized upland black spruce (Mahendrappa and Weetman 1973; Mahendrappa and Salonius 1982), and other species (Miller *et al.* 1976; Paavilainen 1987). The amount of nutrients in needle litter of tamarack was greater than that of black spruce (Fig. 7.1). Comparison of several conifer and deciduous species show similar results (Paavilainen 1984, 1987); Carlyle and Malcolm 1986; Gower *et al.* 1989). Deciduous species may play an important role in nutrient cyling, especially in N fertilized peatlands. This could be beneficial to tamarack and black spruce since both respond to NPK fertilization (chapters 2, 3 and 6).

7.4.2 N, P and K resorption

Foliar NPK of older (>one-year) needles of black spruce was not analysed in the present study. However, assuming seasonal maximum foliar N concentration of 6+-year-old needles was 0.60% (chapter 8), N retranslocation may have been about 54%, which is lower than that of tamarack.

Drainage as well as N_0PK fertilization decreased P resorption for tamarack likely due to increased P availability in the soil. Neither treatment affected resorption of N. The lack of significant treatment effect on resorption of N may be indicative of limited availability of N in plots to which N was not added. In support of this NPK fertilization decreased N resorption, but increased resorption of P and K probably due to dilution.

It appears that N, P and K resorption are partly controlled by foliar N, P and K concentrations which in turn are influenced by soil nutrient availability. This is because resorption of N and P showed strong negative relationships with seasonal maximum foliar N or P concentrations and contents on both sites (Fig. 7.6a,b,c,d). Decreased N and P resorption with fertilization has been found in some studies (Mahendrappa and Weetman 1973; Stachurki and Zimka 1975; Miller *et al.* 1976; Turner 1977) but not in others (Chapin and Kedrowski 1983; Ryan and Borman 1983).

The lack of a significant relationship between K resorption and K concentration and content of tamarack on the undrained site may be related to more leaching of K due to a long period from the onset of

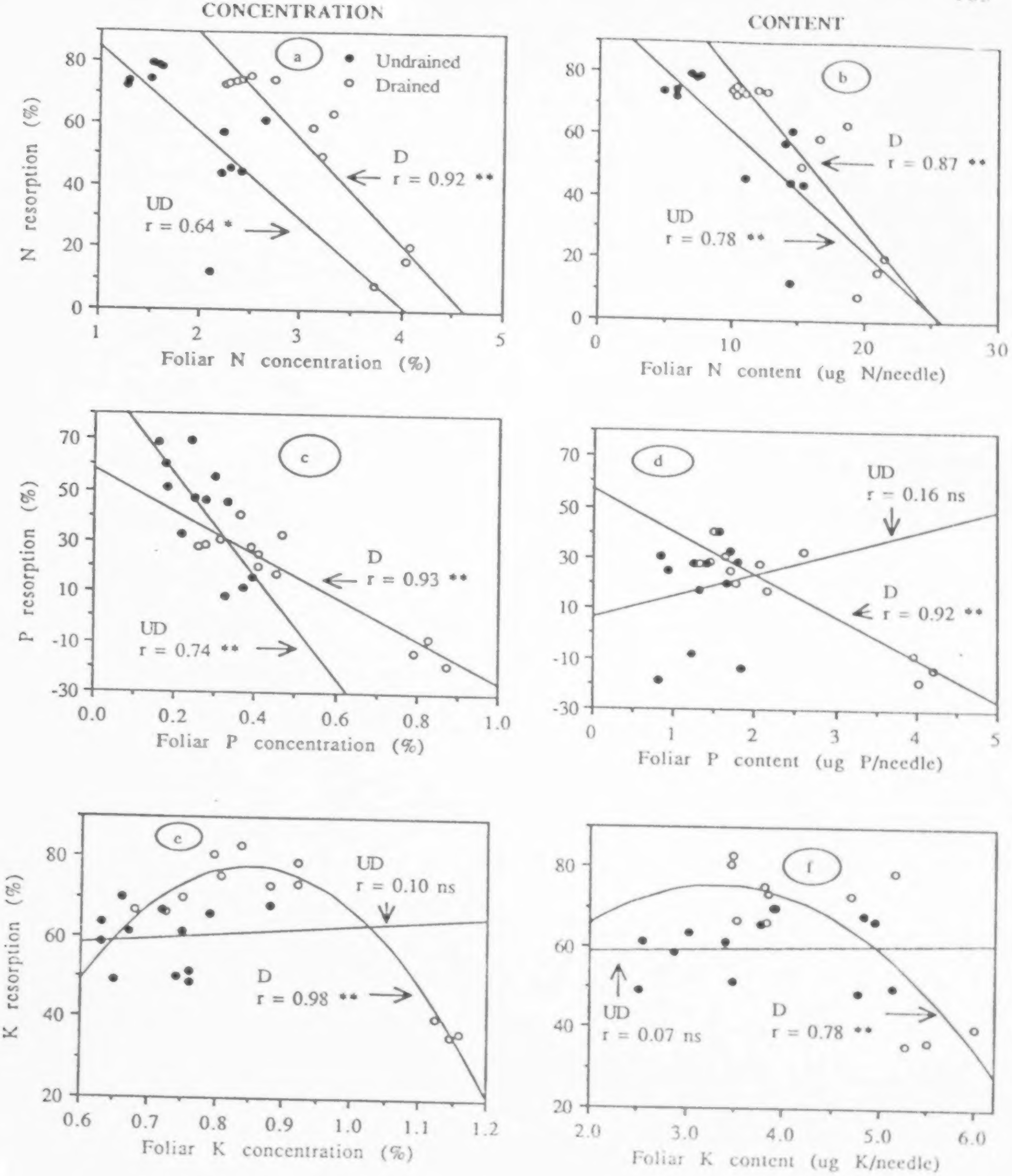

Figure 7.6: N, P and K resoprtion before abscission of needles in relation to foliar seasonal maximum nutrient concentrations and contents for tamarack in response to drainage and NPK fertilization of a minerotrophic peatland at Wolf Creek, central Alberta. UD - undrained site; D - drained site. Significance indicated by ns, * and ** P>0.05, <0.05 and <0.01, respectively.

senescence in early August to needle abscission in late September. However, there are trends for decreased resorption of K with an increase in foliar K on the drained site (Fig. 7.6e,f). My results support Small's (1972) hypothesis that strong nutrient conservation is one of the adaptation mechanisms to nutrient stress. However, the wide distribution of points (Fig. 7.6) suggests that there are other uninvestigated factors that control nutrient resorption before abscission of needle.

Decreased nutrient resorption following fertilization will result in nutrient losses through needle litterfall. P losses from trees may lead to loss from the ecosystem. Vitousek and Reiners (1975) pointed out that such changes in resorption may contribute to increased leakiness of the ecosystem. However, this is not likely for N, especially if mineral N input from decomposing litter is low, because most of the mineral N released will be taken up by live moss (chapter 8).

7.4.3 Needle litter mass per unit nutrient mass

Low availability of nutrients may increase nutrient resorption (Vitousek 1982, 1984). My results are consistent with this general observation. Drainage and/or fertilization increased N and P concentrations of foliage (chapters 2, 3 and 6) and needle litter of tamarack and black spruce, but decreased needle litter dry matter per unit mass of N or P. Similar trends have been reported for other species (Maki 1960; Maggs 1985; Pavilainen 1987).

I found higher N- and P-NMU for black spruce than for the tamarack. This corraborates other comparisons between evergreen and deciduous species (Malkonen 1974, 1977; Paavilainen 1984, 1987; Gower *et al.* 1989) although Gower *et al.* found higher N-MNU in *Larix occidentalis* versus *Pinus contorta* var *latifolia*. These results do not necessarily mean tamarack is less efficient in internal cycling of N This simply reflects a higher N concentration in tamarack foliage. As noted above N resorption was about 80% for unfertilized tamarack as compared to an estimate of 54% for black spruce.

7.5 CONCLUSIONS

Drainage decreased nutrient resorption and subsequently increased needle litter nutrient concentration. On the other hand N fertilization decreased N resorption, but increased resorption of P and K. This seems to suggest that nutrient resorption is partly controlled by foliar nutrient concentration prior to resorption. N fertilization decreased needle litter dry mass per unit mass of N and vice versa for unit mass of P and K.

Drainage and fertilization increased the amount of nutrients returned to the the forest floor through litterfall. The concentration of nutrients in litterfall was higher for tamarack than that for black spruce. This suggests that nutrient turnover will be more rapid in drained and fertilized peatlands. This could be beneficial since more nutrients could be available and taken up by tamarack and black spruce.

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Chapter 8

^{15}N-UREA FERTILIZATION OF A TAMARACK/BLACK SPRUCE MIXED STAND ON A DRAINED MINEROTROPHIC PEATLAND: ^{15}N IN SOIL AND TREE UPTAKE

8.1 INTRODUCTION

Conifer growth in drained peatlands in central Alberta is limited more often by nitrogen than by any other nutrient element (Humphrey 1990; Lieffers and Macdonald 1990; Macdonald and Lieffers 1990; see also chapters 2 and 3). Nitrogen fertilization of drained peatlands resulted in concomitant increases in foliar N concentration and unit needle mass of tamarack and black spruce (see chapters 2 and 3). If these foliar responses are indicative of future stemwood response potential, then N fertilization may be an advantageous management option for successful operational drainage of forested peatlands in central Alberta.

In order to improve the use of fertilizers in forest ecosystems it is necessary to understand the fundamental processes in nutrient uptake and translocation under forest conditions (Mead and Pritchett 1975). There is limited information on these processes in drained boreal peatlands (see Paavilainen 1973). Labelled ^{15}N fertilizer (tracer) technique has been used to quantify distribution, efficiency of uptake and transformations of N (see Nason and Myrold 1991). The method has the advantage that the labelled ^{15}N can readily be identified and determined quantitatively (Melin *et al.* 1983).

Tree nutrient uptake is influenced by several factors including root-mycorrhizal associations. Molina and Trappe (1982) hypothesized that tamarack has greater N uptake potential than black spruce because tamarack forms ectomycorrhizae with genus-specific fungi (more effective mycorrhizal fungi such as *Suillus* spp and *Rhizopogon* spp); whereas black spruce forms ectomycorrhizae with a wide variety of fungi. This seems to suggest that fertilizer N uptake for tamarack may be greater than that of black spruce. However, it is generally accepted that the rate and the amount of nutrient uptake is also a function of, among other things, the size and strength of the aboveground sink (see White 1973; Nambiar 1976; Clement *et al.* 1978; Ingestad 1988). At Wolf

Creek in 1989, when trees of the same breast height diameter (dbh) were compared, the mass of current needles of black spruce was 4 (10 cm dbh) to 11 (2 cm) times higher than that of tamarack (A.G. Mugasha, unpublished data). In addition, black spruce retained photosynthetically active needles of up to 11 or 12 years of age. This seems to suggest that black spruce may have a larger and probably a stronger aboveground sink for N than that of tamarack. In this thesis, I hypothesize that fertilizer N uptake for black spruce is higher than for tamarack.

In mineral soils, tree uptake of N ranged from over 40% of applied N in two growing seasons (Melin and Nommik 1988) to as low as 2% for one season (Preston *et al.* 1990). The amount of N orginating from ammonium and urea fertilizers that is available for tree uptake in organic soils may be significantly reduced through chemical and microbial immobilization (Overrein 1967, 1970, 1972; Nommik 1970; Nommik and Popovic 1971; Paavilainen 1973; Weber and van Cleve 1981; Foster *et al.* 1985). In this thesis, I also hypothesize that the live moss and organic horizons will immobilize a significant quantity of fertilizer N and this may reduce efficiency of fertilizer N uptake.

This study was designed to evaluate seasonal patterns and distribution of ^{15}N-labelled urea fertilizer N in soil, moss layer and foliage of tamarack and black spruce trees on a recently drained minerotrophic peatland. The hypotheses tested were that: a) fertilizer N uptake will be higher for black spruce than for tamarack, and b) immobilization of fertilizer N in live moss and organic soil will reduce the efficiency of fertilizer N uptake. Chapter 9 discusses distribution, uptake efficiency and recovery of fertilizer N in a tamarack/black spruce mixed stand ecosystem.

8.2 MATERIALS AND METHODS

8.2.1 Study area

The ^{15}N-labelled urea fertilizer experiment is part of the Wolf Creek Peatland Drainage Project (53° 25.6' N, 116° 01' W; Appendices 11.9 and 11.16) described in chapter 3. The soil is a Terric Fibric Mesisol

(Agriculture Canada Expert Committee on Soil Survey 1987). The experimental area sloped approximately 1% towards the northeast. Selected soil properties are described in section 8.2.3. The stand description of the two ^{15}N-labelled urea fertilized plots is presented in Table 8.1. Black spruce accounted for over 66% of the stems and over 54% of the basal area. The understory vegetation consisted of the same species as described in chapter 3.

Table 8.1: Stand characteristics of ^{15}N-labelled urea fertilized plots in September 1990, at Wolf Creek, central Alberta.

Species		Stems plot^{-1}	Stems ha^{-1}	Basal area	Dbh	Height
				m^2.ha^{-1}	cm	m
				Plot 1		
Tamarack		71	2730	6.50	5.0(1.5-10.9)[a]	5.46(2.20-9.88)
B. spruce	(a)[b]	64	2460	6.04	5.0(1.6-11.5)	4.38(2.00-8.51)
	(b)	19	730	-	2.2(1.5-2.80)[c]	1.42(0.65-1.81)
	Total	154	5920	12.5	-	-
				Plot 2		
Tamarack		38	1460	4.56	5.7(1.9-14.5)	6.36(2.90-12.0)
B. spruce	(a)	111	4270	6.78	4.1(1.2-10.5)	3.65(1.69-7.11)
	(b)	21	810	-	2.2(1.4-3.10)[c]	1.35(0.80-1.78)
	Total	170	6540	11.3	-	-

[a] Mean with the range in parenthesis;

[b] (a) - black spruce height ≥ 2.00 m and for (b) height <2.00 m;

[c] diameter measured at 0.1 m above ground.

8.2.2 Experimental design and treatments

The experiment involved two treatments replicated twice (Appendix 11.16). The treatments were: a) unfertilized - control, and b) urea fertilized at a dose of 53 kg $N.ha^{-1}$. The urea was isotopically enriched in ^{15}N (2.7761 atom percent excess). The experimental area was selected on the basis of having an acceptable (based on apparent crown vigor) and adequate number of tamarack and black spruce trees. The plots were uniform in terms of understory species composition. The ditch network was excavated with a backhoe in Fall 1987 with parallel ditches 35 m apart and about 90 cm deep.

Four plots were established in August 1988 by isolating each laterally by trenching at the perimeter, except on the ditch side, emplacing a polyethylene sheet (6 mil thick) to a depth of about 50 cm and backfilling. All plots were rectangular in shape and each unfertilized plot measured 13 by 33 m, while each fertilized plot measured 13 by 20 m with the smaller dimension at the edge of a drainage ditch. The dbh and height of all trees were taken using a diameter tape and a telescopic pole respectively. For trees less than 2.0 m height, diameter was measured at 0.1 m above the ground.

^{15}N-labelled urea was dissolved in 50 L of water and sprayed as uniformly as possible on the moss surface of each fertilized plot on June 1, 1989 using a pressurized sprayer. This was achieved by making multiple perpendicular traverses in alternate directions. At the same time, an equivalent of 80 $kg.ha^{-1}$ of phosphorus as triple superphosphate and 120 $kg.ha^{-1}$ of potassium as potassium chloride was broadcast onto each fertilized plot.

Fertilizer application was carried out about nine days after bud break in tamarack and about two and one-half weeks before bud break in black spruce.

8.2.3 Soil sampling and analysis for study area characterization

Soil samples were taken to 60 cm depth for characterization of the experimental area in July 1988. Ten soil cores per plot were randomly selected from mid-positions between hollow and hummock microrelief. Following sampling, soil taken from peat stock piles (the spoil) near the edge of a drainage ditch was used to fill holes created during sampling to minimize physical disturbances to the forest floor. Some selected soil characteristics are presented in Table 8.2. Peat thickness was measured at a minimum of 10 randomly selected points in the vicinity of each plot as described in chapter 3. Mean peat thickness in July 1988 was 95 ± 9 (SD) cm.

Table 8.2: Means of selected soil properties[a] of the ^{15}N-labelled urea experiment at Wolf Creek, central Alberta.

Soil depth	Bulk density	Electrical conduct.	pH(H2O)	Total C	Total N	Organic P
cm	$Mg.m^{-3}$	$dS.m^{-1}$		-----------%-----------------		
0-10[b]	0.02	0.22	4.6	48.0	1.1	0.09
10-20	0.06	0.16	5.8	44.7	1.3	0.10
20-30	0.13	0.11	5.9	45.3	2.1	0.12
30-40	0.16	0.10	5.8	45.8	2.1	0.11
40-50	0.18	0.06	5.8	47.9	2.1	0.09
50-60	-	0.06	5.8	48.1	2.1	0.08

[a] Number of observations (n) per increment for bulk density was 20, and n=2 for other variables;

[b] Measured from the surface of live moss.

8.2.4 Seasonal sampling of soil and tree foliage

Following fertilizer applications the soil was sampled three times, tree foliage four times, and tree needle litter once (Table 8.3).

Table 8.3: Timetable for soil, and tamarack and black spruce foliage sampling in ^{15}N-labelled urea fertilized and unfertilized plots at Wolf Creek, central Alberta.

Date	Period after fert. (wk)[a]	Component sampled
June 12 1989	2	Foliage (both species) and soil
July 5	5	Foliage (both species) and soil
August 31[b]	13	Foliage (both species) and soil
September 30	17.5	Foliage (tamarack)
October 14	19.5	Foliage (black spruce)

[a] approximate time;
[b] Intensive sampling.

Sampling was designed to provide frequent observations during the first growing season since the ecosystem distribution of ^{15}N was expected to be more dynamic (Nason 1989).

Five trees per species per plot representing a range of diameter classes were selected and tagged in September 1988 for future foliar sampling. To minimize the edge effect (Melin and Nommik 1988; Nason *et al.* 1990), selected trees were over 2 m distance from the perimeter of the plot. Foliage was sampled as described in chapter 3. Following each sampling, short-shoot needles of tamarack and current and one-year-old needles of black spruce were sealed in polyethylene bags by tree and stored at -20 °C.

Intensive sampling of trees was carried out on 31 August 1989. For each of the five preselected trees, branch samples were taken from upper one third, middle one third and lower one third crown positions, hereafter referred to as upper, middle and lower crown positions. For tamarack, short-shoot needles from each crown position were separately bagged by tree and stored as described above. For black spruce, needles from each crown position were separated by age (current year - C, C+1, C+2, C+3, C+4, C+5, C+6+older), bagged by tree and by needle age and stored at -20 °C.

On each soil sampling date five cores (8.1 x 8.1 cm horizontal cross-section) were taken per plot. Each core was divided into 0 to 5 cm (live green moss plus other small plants), 5 to 10 (brown moss) and thereafter 10 cm increments to 40 cm depth. However, on 31 August 1989 samples were taken to 60 cm depth. On each sampling date, soil samples taken from the same depth increment and same plot were composited, and field moist subsamples were frozen (-20°C) for future analysis. Sample holes were backfilled as described in section 8.2.3.

8.2.5 Chemical analysis of soil and foliar samples

Soil and plant ^{15}N-labelled urea fertilized and unfertilized materials were analysed as follows. Unfertilized materials were taken from the vicinity of the ^{15}N plots in order to determine the natural abundance for each soil and tree component. Prior to chemical analyses, all tree branch/twig samples were dried at 65 °C for 24 to 36 h and allowed to equilibrate at room temperature and humidity. Thereafter, needles and twigs were separated, and mean weight per needle determined from four subsamples of 100 needles. Foliar subsamples were ground to pass a 20 mesh sieve. Then the ground subsamples were pulverized in a vibrating-ball mill (Retsch, Type MM2, Brinkmann Instruments Co., Toronto, Ontario, Canada), as required for sample preparation for mass spectrometer analysis. Ethanol was used to chemically clean the mill between samples after vacuum cleaning (Binkley *et al.* 1985).

After thawing and manual homogenizing, moist equivalent subsamples of about 3 to 6 g dry (105°C) soil were shaken with 1.92 M KCl at a soil:solution ratio range of 1:38 to 1:15 for 2 h. Because a minimum of 50 *u*g N per sample is required for N by the Dumas method, the mass of extracted peat subsamples was increased for profile samples of lowest mineral N. The peat residue from the KCl extract, hereafter referred to as peat residual, was washed with deionized water until the KCl filtrate formed no white precipitate with silver nitrate solution, then dried at 65

°C for 36 h and ground to pass a 20 mesh sieve before final pulverization with the ball-vibrating mill as described above. Since preliminary analysis of the extract by auto analyser (Technicon Instruments 1977) indicated that there were only trace amounts of nitrate/nitrite was reduced to ammonium and all extracts were analysed for ammonium only. Ammonium in the KCl extract was recovered by the diffusion procedure as modified from Turner and Bergersen (1980).

All plant, soil and diffused ammonium samples were analysed for total N and ^{15}N abundance using an Automatic Nitrogen Analyser (ANA) 1500 coupled to a Stable Isotope Ratio Analyser (SIRA) 10 Mass Spectrometer (VG Inorganic, Astonway, Middlewich, Cheshire, England) which comprises an automated Dumas system (Carlo Erba) for total N and a flow-through system of the nitrogen gas so generated for isotope ratio analysis using a triple collector system.

8.2.6 Data analysis

8.2.6.1 Percent ^{15}N-fertilizer in soil and plant components

The percent of ^{15}N-fertilizer in soil and plant components was calculated from ^{15}N abundance in soil or plant tissue samples using equation 8.1.

$$\%\ \text{NDFF} = (\text{atom}\ \%\ ^{15}\text{N excess in sample}/2.7761) \times 100 \qquad 8.1$$

where: %NDFF - the percent of N derived from fertilizer
2.7761 - atom percent excess of ^{15}N in urea solution

The atom percent excess of ^{15}N in soil and plant tissue samples was calculated as the difference between ^{15}N abundance of fertilized soil or needles and of respective unfertilized soil and needles.

8.2.6.2 Statistical analysis

The plant and soil data were analysed with aid of a microcomputer using the general linear models (GLM) procedure of SAS (SAS Inst. Inc. 1987). Only the data from ^{15}N-labelled urea plots were analysed. This is because the ^{15}N atom percent excess was used to estimate the percent of N derived from fertilizer in soil and needles.

The tree foliar data were sorted by date, species, crown position and needle age. Then one way ANOVA was employed to evaluate: a) the effect of sampling date on foliar attributes (total N concentration and content, %NDFF, and ^{15}N content) of current and one-year-old needles from upper crown position of tamarack and black spruce, and b) the effect of needle age on foliar attributes of black spruce within each crown position. Prior to ANOVA, the null hypothesis for homogeneity of variance for each error term was tested by the Shapiro-Wilk procedure (SAS Inst. Inc. 1987) and was not rejected.

The ANOVA was also employed to evaluate the effect of sampling date and soil depth on attributes of peat residual and mineral-N. The effects of sampling date and soil depth were analysed using a split-plot design: sampling date - main factor, and soil depth - subfactor. However, attributes of residual peat and mineral-N error variances were heterogenous. The Box and Cox (1964) procedure was used to select the appropriate transformation for each response variable.

The unpaired t-test was used to evaluate differences between black spruce and tamarack foliar attributes of 1989. To evaluate the effect of crown position on foliar attributes the data were sorted by species and needle age. For each data subset, foliar attributes of each needle age class were subjected to a paired t-test of two crown positions (i.e., upper vs. middle, upper vs. lower, middle vs. lower). The relationship between foliar total N concentration and content, %NDFF and ^{15}N content was evaluated using the Pearson correlation analysis.

One of the objectives of this study was to examine patterns of fertilizer N uptake by the two tree species. In addition to this objective I was interested in the examination of the relationship between tree attributes and fertilizer N uptake. In order to test this relationship, foliar N attributes and tree dbh, total height (Ht) and sapwood cross-

Table 8.4: Allometric equations of tree breast height diameter (dbh) and sapwood cross-sectional area at bh (SP) for tamarack (n = 35) and black spruce (n = 27)[x], at Wolf Creek, central Alberta.

Species	a[y]	b	EMS	R^2
Tamarack	0.649	0.453	0.0120	0.93
B. spruce	0.321	0.569	0.0080	0.97

[x] Equations follow equation: $\log (y) = a + b \log (x)$, where x = dbh (cm) and y = SP (cm^2). Mean characteristics of the trees are given in Appendix 11.19.

[y] All intercepts were corrected for bias that occurs when converting from logarithmic units (Baskerville 1972).

area at 1.3 m aboveground (SP), the data of 31 August 1989 were sorted by species and each data subset was subjected to the Pearson correlation analysis. Tree SP was calculated with the relationships developed previously for tamarack and black spruce trees sampled in the vicinity of ^{15}N-labelled urea plots (A.G. Mugasha, unpublished data, Table 8.4).

8.3 RESULTS

8.3.1 Effect of tree size on ^{15}N fertilizer uptake

For tamarack, dbh and sapwood cross-sectional area at breast height (SP) on 31 August 1989 were negatively correlated ($P<0.05$) with foliar total N concentration pooled for all crown positions (Table 8.5). There was no significant ($P>0.05$) relation between dbh, height and SP for foliar N content, %NDFF and ^{15}N content. For black spruce in both years, these correlations were not significant ($P>0.05$). These results show in general that: a) increased tamarack dbh and SP was associated with reduced foliar N concentration, but uptake of NH_4^+-^{15}N is independent of tree size; and b) foliar N concentration and uptake of NH_4^+-^{15}N urea are independent of tree size for black spruce.

Table 8.5: Pearson correlation coefficients describing the relationship among tree breast height diameter (Dbh), total height (Ht), sapwood cross-sectional area at dbh (SP) and foliar N attributes[1] of ^{15}N-fertilized tamarack and black spruce[2] on a minerotrophic peatland at Wolf Creek, central Alberta.

	1989				1990			
	N	Nc	%NDFF	^{15}Nc	N	Nc	%NDFF	^{15}Nc
				Tamarack				
Dbh	-0.31*[3]	-0.19	-0.26	0.14	-0.39*	-0.02	0.50*	0.42*
Ht	-0.08	-0.01	0.16	0.14	-0.31*	0.15	0.43*	0.46*
SP	-0.35*	-0.20	-0.22	0.11	-0.38*	-0.04	0.48*	0.40*
				Black spruce				
Dbh	-0.05	0.08	-0.07	-0.03	-0.08	-0.03	-0.03	-0.05
Ht	-0.03	0.05	-0.14	-0.09	-0.09	-0.13	-0.05	-0.11
SP	-0.03	0.08	-0.05	-0.02	-0.07	-0.03	-0.03	-0.05

[1] N - foliar total N concentration (% dry wt.), Nc - foliar N content (*u*g N.needle^{-1}), %NDFF - percent of foliar N derived from fertilizer, and ^{15}Nc - foliar ^{15}N content (*u*g ^{15}N.needle^{-1}).

[2] Number of observations were 33 (1989) and 30 (1990) for tamarack, and 136 (1989) and 143 (1990) for black spruce. For each species data were pooled for all crown positions and needle age.

[3] Significance indicated by * for $P \leq 0.05$.

8.3.2 Seasonal patterns of total N and ^{15}N in soil and tree foliage

8.3.2.1 Total N and ^{15}N in soil

The effect of sampling date on N attributes of peat residue was not significant (P<0.31, Fig. 8.1a,c), but that of soil depth was significant

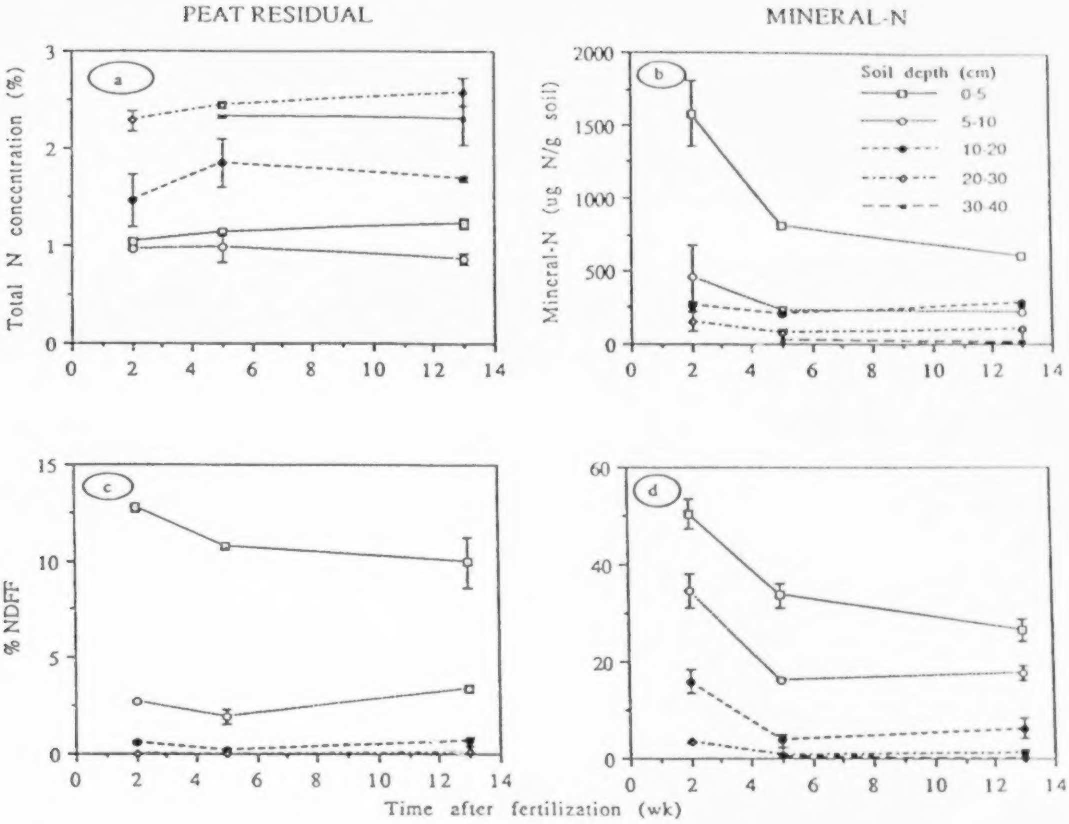

Figure 8.1: Total N concentration and percent of nitrogen derived from fertilizer in peat residual from KCl extract and washing with deionized water, and total mineral N content and percent of nitrogen derived from fertilizer in the total mineral-N over time after fertilization. The site at Wolf Creek, central Alberta was fertilized with ^{15}N-labelled urea at the dose of 53 kg N.ha^{-1} on 1 June 1989. One arm of an error bar indicates the standard error of the mean of two plots.

(P<0.01). A greater proportion of ^{15}N-labelled urea fertilizer was retained (P<0.001) within 0-20 cm depth, and the live moss layer (0-5 cm) was consistently most highly enriched.

Patterns of mineral-N with sampling date and soil depth are presented in Fig. 8.1b,d. The effects of sampling date and depth on the concentration and %NDFF of mineral-N were significant (P<0.002). The concentration of mineral-N and %NDFF were highest within the live moss and decreased sharply with depth (Fig. 8.1b,d).

The concentration of mineral-N and %NDFF within 0 - 20 cm depths were highest at two weeks after fertilization, but declined rapidly from week 2 to 5, and then declined gradually or remained unchanged thereafter. Mean mineral-N weighted by bulk density in the 0 - 30 cm depth was 295 mg N.kg^{-1} at week 2, but it dropped to 175 mg N.kg^{-1} at week 5 and was 194 mg N.kg^{-1} after 13 weeks following fertilization. Mineral-^{15}N in 0 - 30 cm depth was 76 mg N.kg^{-1} at week 2 but dropped to 21 mg N.kg^{-1} at week five and was 19 mg N.kg^{-1} after 13 weeks.

8.3.2.2 Tree foliar total N and ^{15}N

Seasonal patterns of foliar total N concentration and content in needles of tamarack and black spruce (Fig. 8.2) followed trends similar to those described in chapter 6.

The effect of sampling date on foliar %NDFF and ^{15}N content of needles formed in 1988 for black spruce and in 1989 for tamarack and black spruce was significant (P<0.001, Table 8.6; Fig. 8.2). For both species, the presence of fertilizer N (as indicated by ^{15}N) was detected in foliage at 2 weeks following fertilization (Fig. 8.2), when the first sampling was done. Thereafter, ^{15}N fertilizer in foliage increased rapidly until mid-October 1989 when sampling of black spruce needles was terminated. For tamarack, increased ^{15}N to late August was followed by a slight decline during needle senescence.

The %NDFF of tamarack needles was significantly (P<0.001) lower than that of black spruce throughout the study period (Fig. 8.2). These results suggest that tamarack is not as efficient as black spruce in taking up N fertilizer.

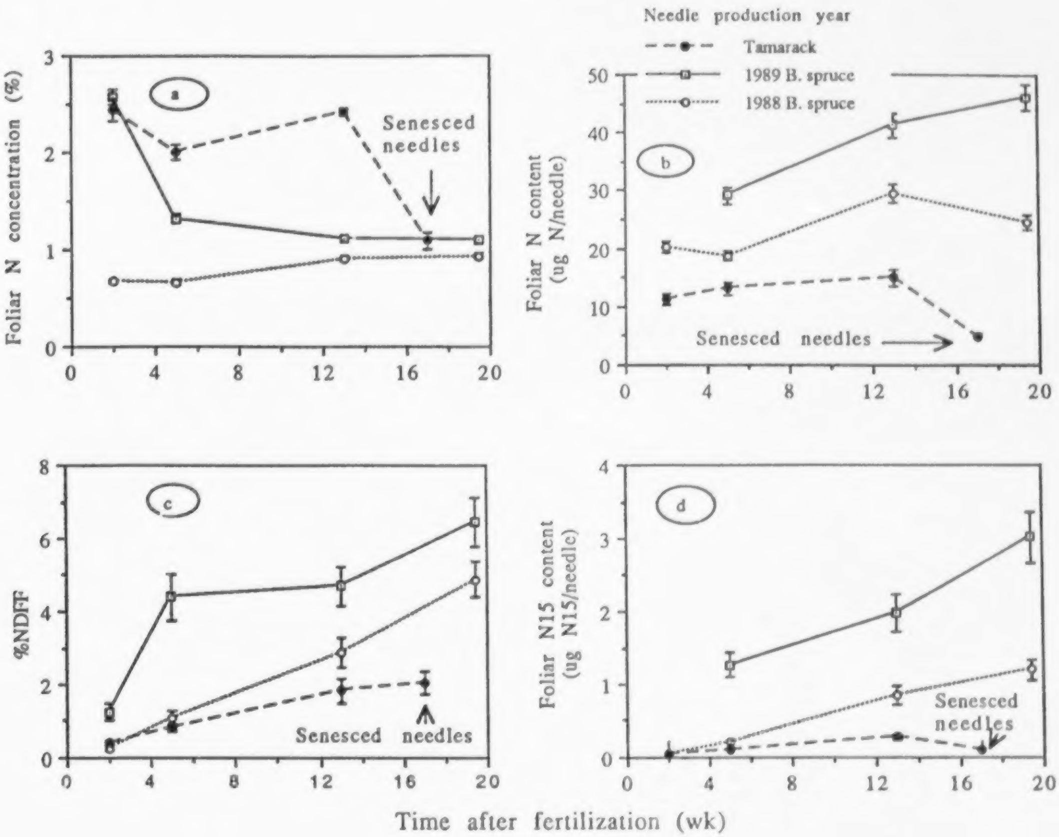

Figure 8.2: Changes in foliar total nitrogen concentration and content, percent of nitrogen derived from fertilizer and ^{15}N content of needles of tamarack and black spruce over time after fertilization of a drained minerotrophic peatland with ^{15}N-labelled urea applied at the dose of 53 kg N.ha^{-1} on 1 June 1989 at Wolf Creek, central Alberta. Foliar samples were taken from upper crown position. One arm of an error bar indicates the standard error of the mean of ten trees.

Table 8.6: Summary of ANOVA of seasonal patterns of foliar attributes of ^{15}N-labelled urea fertilized tamarack and black spruce on a drained minerotrophic peatland in 1989, at Wolf Creek, central Alberta.

Foliar attribute	ANOVA of sampling date[1]					
	MS	Error	P>F	MS	Error	P>F
	Tamarack					
Needle mass	0.14	0.026	0.004	-	-	-
N concn.	4.22	0.0.73	<0.001	-	-	-
N content	210	12.2	<0.001	-	-	-
%NDFF	6.47	0.50	<0.001	-	-	-
^{15}N content	0.097	0.007	<0.001	-	-	-
	B. spruce in 1988			B. spruce in 1989		
Needle mass	10.7	0.33	<0.001	1.17	0.31	0.020
N concn.	4.19	0.022	<0.001	0.21	0.006	<0.001
N content	762	39.0	<0.001	222	13.2	<0.001
%NDFF	1.69	2.87	<0.001	42.2	1.13	<0.001
^{15}N content	7.76	0.72	<0.001	2.93	0.10	<0.001

[1] Degrees of freedom for date and error tamarack needles and one-year-old needle of black spruce were 3 and 33, respectively; for current needles of black spruce were 3 and 36, respectively.

8.3.3 Effect of crown position and needle age on foliar attributes

The effects of crown position and needle age on foliar N concentration and content, %NDFF and ^{15}N content of tamarack and black spruce were evaluated from samples taken on 31 August 1989 (thirteen weeks after urea application). In general the effect of crown position on all foliar N and ^{15}N attributes of tamarack was not significant (P>0.05, paired t-test, results not presented), indicating a uniform sink for N.

For black spruce, foliar total N concentration within each needle age class did not vary with crown position (P>0.05, Appendix 11.17; Fig. 8.3), except for C+6 and older needles where N concentration decreased (P=0.02) from lower to middle crown position. On the other hand, N content generally decreased from upper to lower crown position largely due to an increase in unit needle mass from upper to lower crown positions. For black spruce, %NDFF and ^{15}N content of current and C+6 and older needles decreased from upper to middle crown position (Fig. 8.3c,d).

For each crown position of black spruce, foliar N concentration decreased with needle age (Fig. 8.3 a,b). However, other foliar attributes of black spruce decreased (P<0.02, Appendix 11.18; Figs. 8.3c,d) from current to one-year-old needles on 31 August 1989.

Foliar total N concentration and content were significantly positively correlated with foliar %NDFF (P<0.01) for black spruce. To the contrary, these correlations were negative but not significant (P>0.05) for tamarack (results not presented). These results suggest that for black spruce more fertilizer N is allocated to tissues with already high N content, usually young tissues. The nonsignificant correlations between foliar attributes of tamarack suggest uniform distribution of fertilizer N within the tree crown.

8.4 DISCUSSION

8.4.1 Seasonal patterns of total N and ^{15}N in soil and tree foliage

8.4.1.1 Total N and ^{15}N in soil

My findings of high retention of NH_4^+-N in live moss are consistent with those reported in Alaska by Weber and van Cleve (1981). They observed that 28 months after isotope application (3.23 - 4.12 kg $N.ha^{-1}$) the feather moss layer was highly enriched. They speculated that this indicates tight internal N cycling within the feather

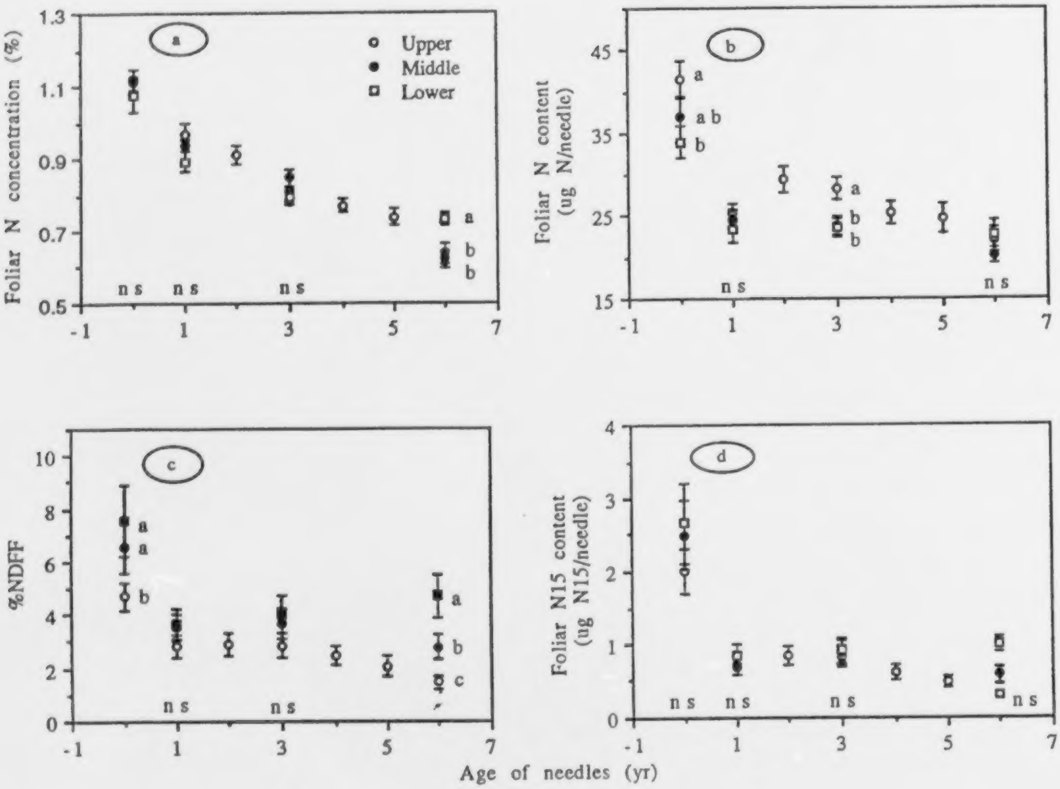

Figure 8.3: Effect of crown position and needle age on black spruce foliar nitrogen concentration, N content, percent of nitrogen derived from fertilizer and ^{15}N content for black spruce sampled on 31 August 1989 after fertilization of a drained minerotrophic peatland with ^{15}N-labelled urea applied at the dose of 53 kg N.ha^{-1} on 1 June 1989. Age six includes older needles. One arm of an error bar indicates the standard error of the mean of ten trees. Means followed by the same letter are not significantly different ($P<0.05$); ns = crown positions not significantly different ($P>0.05$).

moss layer or tying up nitrogen in unavailable forms. The strong ability of live moss layers and organic horizons to retain NH_4^+-N when ammonium or urea-based fertilizers are applied at low doses may be disadvantageous from a tree growth point of view since less fertilizer may be available for tree uptake in the short term. However, in the long term, this fertilizer N may be available for tree uptake through mineralization.

Total amount of mineral-N (calculated from mineral-N concentration (Fig. 8.1) and soil mass) held in the 0 - 30 cm layer at week two dropped by 35% after 13 weeks following fertilization. On the other hand, mineral-^{15}N decreased by 78% within the same period. This change in fertilizer mineral-N over time may be related to: a) gaseous losses - during the first two weeks following fertilization NH_3 volatilization was about 4.6 kg N.ha^{-1} (<8.7% of applied N, see Table 9.6 of chapter 9); b) leaching beyond the sampled depth during the first four weeks since there was higher rainfall (131 mm, see chapter 3) as compared to a normal of 80 mm (Env. Can. n.d.)), but this was unlikely as discussed below; c) uptake by tree and understory vegetation since %NDFF in tamarack and black spruce foliage increased over time; and d) $NH4^+$-N initially held on cation exchange sites of live moss and peat may have undergone biochemical reactions to become partly non-exchangeable (Nommik 1970; Overrein 1967, 1970, 1972). The slight increase in %NDFF of peat residual within the 5 - 20 cm depth from July to August 1989 (Fig. 8.1c) suggests $NH4^+$-N fixation by peat. The high retention of fertilizer within the 0-10 cm depth suggests that mineral-N leaching was also not the source of decreased mineral-N derived from fertilizer. Nitrate leaching was improbable since KCl extracts contained only trace amounts of NO_3^--N in any of the depth increments.

8.4.1.2 Tree foliar ^{15}N

Seasonal foliar ^{15}N patterns of black spruce in 1989 are similar to those reported for other conifers (Mead and Pritchett 1975; Heilman *et al.* 1982; Nambiar and Bowen 1986; Melin and Nommik 1988; Preston *et al.* 1990). The significantly lower %NDFF of tamarack as compared to that of black spruce needles throughout the study period is in agreement with my hypothesis. These results are in sharp contrast with the hypothesis of Molina and Trappe (1982) that tamarack has greater N uptake potential than black spruce. My results suggest that the higher foliar total N concentration in needles of semi-mature tamarack may be related to some other mechanisms such as a greater ability for N conservation, efficient internal N cycling or storage.

Near the end of the first growing season the %NDFF was about 7% in current and 5% in one-year-old needles for black spruce. These results are similar to those of $(NH_4)_2SO_4$ fertilized *Pinus elliottii* var *elliottii* (Mead and Pritchett 1975), but slightly lower than that of urea fertilized *P. contorta* var *latifolia* (Preston *et al.* 1990) and *P. sylvestris and Picea abies* (Melin and Nommik (1988). The lower %NDFF reported by Mead and Pritchett (1975) was probably due to low dose of N applied and to intensive leaching. On the other hand, the higher %NDFF reported by Melin and Nommik (1988) and Preston *et al.* (1990) may be related to high doses of N applied. For my study, the low dose of N and high retention of N by live moss and organic soil may explain the observed low %NDFF for black spruce.

8.4.2 Effect of crown position and needle age on foliar attributes

My findings of lack of a relationship between foliar N concentration and crown position of tamarack are similar to those reported for tamarack in Minnesota (Tyrrell and Boerner 1987). I am not aware of any study that evaluated the distribution of ^{15}N-labelled fertilizer in relation to crown position of tamarack. For black spruce, foliar total N concentration within each needle age class did not vary with crown position, except for C+6+older needles. Total nitrogen concentration of current and one-year-old needles of black spruce (Lowry and Avard 1968) and *Pinus sylvestris* (Paavilainen 1973) increased from upper to lower crown position, but that of *Pinus elliottii* did not vary with crown position (Mead and Pritchett 1975).

My findings of increased foliar ^{15}N attributes of current needles from middle to upper crown position for black spruce coincides with results of other evergreen conifers (Paavilainen 1973; Worsnop and Will 1980; Melin *et al.* 1983). To the contrary, ^{15}N concentration was higher in the lower than in upper crown position of *Pinus elliottii* (Mead and Pritchett 1975). They theorized that as the ^{15}N moves up the crown it becomes further diluted with nutrients cyling internally within the tree. For my study, the higher foliar ^{15}N in the upper crown suggests that the upper crown position of black spruce is the stronger sink for ^{15}N than other crown positions.

Foliar N concentration decreased with needle age. Similar results for black spruce have been reported elsewhere (Weetman 1968; Lowry and Avard 1968; Small 1972; Hom and Oechel 1983, K. Greenway 1991 - personal communication). However, foliar total N concentration for *Pinus sylvestris* did not change with needle age (Paavilainen 1973).

For all crown positions foliar ^{15}N attributes decreased from current to one-year-old needles of black spruce. Decreased foliar %NDFF and ^{15}N content with needle age have been observed for other conifers (Nommik 1966; Bjorkman *et al.* 1967; Mead and Pritchett 1975; Heilman *et al.* 1982; Melin *et al.* 1983; Nambiar and Bowen 1986; Preston *et al.* 1990). The higher ^{15}N accumulation in young relative to older needles of conifers may be related to the higher rate of metabolic activity of the former and relatively slow translocation of N in trees (Nommik 1966; Mead and Pritchett 1975). Mead and Pritchett (1975) observed that young developing leaves require high amounts of N for protein synthesis; while older foliage requires little additional N because photosynthesis is their major function. Nommik (1966) observed that these trends of foliar ^{15}N attributes may indicate either a relatively slow rate of continuous breakdown and resynthesis of cellular proteins or a slow rate of transport and redistribution of mobile nitrogen within the plant. He also suggested that uneven distribution of ^{15}N in tree tissue of different ages was indicative of an unstationary state, as regards to the N turnover in the entire plant.

8.5 CONCLUSIONS

a) Fertilizer N immobilized in peat residue did not change during the study period. To the contrary, fertilizer N decreased rapidly from week 2 to 5 and then decreased gradually thereafter. These trends may be related to: i) volatilization of $^{15}NH_3$, ii) uptake by plants, iii) immobilization by micro-organisms, and iv) $^{15}NH_4^+$-N held on exchange sites undergoing biochemical reactions to become partly non-exchangeable.

b) Fertilizer N showed little vertical mobility in soil, and tended to be retained within 0-20 cm depth. The ability of live moss and near-surface peat to retain $^{15}NH_4^+$-N is related to their high cation exchange capacity, tight internal cycling of N and tying up of N in a non-exchangeable form.

c) As expected, foliar %NDFF and ^{15}N content of both tamarack and black spruce current and one-year-old needles increased rapidly during the first growing season.

d) For black spruce in 1989, foliar %NDFF and ^{15}N content of current needles was greatest in the upper crown position. This result suggests: i) allocation of more fertilizer N to more metabolically active tissues, and ii) limited uptake of fertilizer N may have led to less ^{15}N being available to needles in middle and lower crown positions.

e) Crown position had no effect on foliar N concentration, %NDFF and ^{15}N content of tamarack because: i) on a whole tree basis, tamarack has less needle mass than black spruce (about 8 factor; for trees of the same dbh), and ii) all needles of tamarack are of the same age (except long-shoot needles not included in my samples) and are not as shaded as in black spruce. Consequently, metabolic activity and N demand by tamarack needles from all crown positions apparently were the same.

f) As expected for black spruce, needles of presumed highest metabolic activity (i.e., current and one-year-old needles) contained more N derived from fertilizer than older needles.

g) Black spruce had a higher percentage of N derived from fertilizer than did tamarack. This may be related to low needle mass (smaller sink) and initially higher foliar N concentration for tamarack that may have induced less ^{15}N uptake. For black spruce, high needle mass (bigger sink) and moderate deficiency of N may have enhanced fertilizer N uptake. The initially high foliar N concentration of tamarack needles was presumably not due to higher uptake of fertilizer N, but due to higher efficiency for conservation, i.e., greater resorption of N before needle senescence (see chapter 7) and internal cycling.

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Chapter 9

DISTRIBUTION AND RECOVERY OF ^{15}N-UREA IN A TAMARACK/BLACK SPRUCE MIXED STAND ON A DRAINED MINEROTROPHIC PEATLAND

9.1 INTRODUCTION

Conifers on drained peatland in western Canada are limited in their growth by N and sometimes P, K and S (Humphrey 1990; Lieffers and Macdonald 1990; Macdonald and Lieffers 1990; see chapters 2, 3, 4 and 6). Nitrogen fertilization of drained peatlands resulted in some positive foliar responses of tamarack (*Larix laricina* (Du Roi) Koch.) and black spruce (*Picea mariana* (B.S.P.) Mill.) (see chapters 2, 3, 5 and 6). The use of N fertilizers to improve growth of conifers in drained peatlands in western Canada has been carried out only experimentally, but the potential for significant increase in tree growth through drainage and fertilization is increasing gradually. This requires a better understanding of the uptake efficiency, distribution and recovery of applied fertilizer within the forest ecosystem in order to improve the effectiveness of fertilization.

The study reported here used ^{15}N-labelled urea fertilizer to determine the distribution of and recovery of fertilizer N in above- and below-ground tamarack/black spruce ecosystem components. My working hypotheses were that a relatively high proportion of fertilizer N will be: a) retained in near-surface soil layer; b) allocated to metabolically active tree components, and c) taken up by black spruce versus that of tamarack since black spruce has a higher foliar mass (bigger sink for N) than tamarack (see chapter 8).

9.2 MATERIALS AND METHODS

9.2.1 Study area and experimental design

The experimental area and experimental design were described in chapters 3 and 8.

9.2.2 Sampling and analysis of plant and soil

Tree foliage and soil intensive sampling on 31 August 1989 and analysis protocols are described in chapter 8. The second intensive sampling of tree foliage and soil was on 2 September 1990. Samples were taken from five preselected trees per species per plot. Stemwood increment cores (sapwood plus heartwood) and stembark (including cambium) at about 1.3 m above the live moss surface, and roots were also taken from preselected trees on both dates. Near-surface roots were taken by excavating at the base of a tree stem and following each exposed root for up to 1 m distance before severing it and whole 1 m root taken. On each sampling date, stemwood increment cores, stembark and tree root samples were separately pooled by plot, and stored at -20 °C. In additional to tree samples, on each sampling date the understory vegetation was clipped at ground level from five randomly selected 0.01 m^2 square microplots per plot, sorted by species, sealed in polyethylene bags and stored at -20 °C. In the laboratory, shrub and herb samples were dried at 70 °C, and separated into foliage and stems plus twigs. All tree and understory vegetation component subsamples were ground and analysed as described in chapter 8.

9.2.3 Data analysis

The data were analysed with aid of a microcomputer using SAS-PC software (SAS Inst. Inc. 1987), and procedures were the same as those described in chapter 8. The ^{15}N content of any plant or soil component was calculated as a product of component total N content (mass of N per given component) x percent nitrogen derived from fertilizer (%NDFF). The mass of each tree component was estimated using the allometric equations developed previously for tamarack and black spruce adjacent to the experimental area (Table 9.1). For black spruce, the contribution of each needle age class to total needle biomass was estimated using the needle mass - needle age relationship developed previously (Table 9.2). The ^{15}N content for each needle age class per tree was then calculated. On a plot level, biomass, total N content and ^{15}N content for each aboveground tree component was obtained by summation of individual tree component biomass or total N content or ^{15}N content. These tree component totals were converted to a stand level. Paired t-tests were used to evaluate differences between black spruce and tamarack aboveground component biomass, total N and ^{15}N content on a stand level.

9.3 RESULTS

9.3.1 Distribution of tree biomass and nitrogen content

Detailed information on foliar N concentration and content, and ^{15}N status for tamarack and black spruce in 1989 is presented in chapter 8. Corresponding values for twigs, stembark and roots for both species in 1989 and 1990 are presented in Appendix 11.20.

The distribution of the aboveground tree component biomass and nitrogen content is given in Table 9.3. In both years, foliage biomass of tamarack averaged about 2% and that of black spruce about 14% of the total standing aboveground tree biomass. For black spruce, current year needles accounted for a greater proportion of the needle biomass relative to other annual needle age classes in 1989 and 1990. For tamarack, branches (wood plus bark) and stembark contributed about 12.6% of the total standing tree biomass. The contribution by corresponding black spruce components was 17.6%.

At a stand level, boveground components of tamarack contained relatively less total nitrogen compared to black spruce (Table 9.3). For tamarack in 1989, nitrogen content was 16.4% in foliage, 12.9% in branches and 6.0% in stembark of the total nitrogen contained in aboveground tree components, excluding the stemwood. In 1990, corresponding contributions were 14.1, 12.7 and 4.6%, respectively,

Table 9.1: Allometric equations[s] of tree component biomass for tamarack (n = 35) and black spruce 2 m height (n = 22) and >2 m height (n = 26) at Wolf Creek, central Alberta. (Source: A.G. Mugasha, unpublished data.)

Tree Component	a[t]	b	EMS[u]	r^2	Mean Dev.[v]
	Tamarack				
Stemwood	-2.566	2.246	0.02570	0.974	-2.35
Stembark	-3.805	2.002	0.03454	0.957	-2.82
Branches[d]	-4.309	2.369	0.02503	0.911	6.16
Foliage	-5.202	2.178	0.07928	0.920	-1.07
Total aboveground tree	-2.143	2.229	0.02568	0.974	-1.50
	Black spruce <2 m height				
Stemwood	2.001	2.940	0.0344	0.904	-3.40
Stembark	1.974	2.258	0.0321	0.855	-3.10
Branches[w]	2.636	2.210	0.0983	0.649	-9.89
Foliage	3.291	2.181	0.0867	0.672	-8.94
Total aboveground tree	4.019	2.365	0.0454	0.821	-4.49
	Black spruce >2 m height				
Stemwood	-2.926	2.194	0.04382	0.966	1.94
Stembark	-3.485	1.837	0.04941	0.946	-0.98
Branches[d]	-3.019	1.798	0.13150	0.863	4.87
Foliage	-2.193	1.487	0.09222	0.861	0.85
Total aboveground tree	-1.499	1.951	0.05088	0.951	2.33

[s] Equations follow the general form: $\ln (x) = a + b \ln (y)$; where x = component mass in kg and y = dbh for tamarack and black spruce > 2 m or basal diameter for black spruce < 2 m, in cm. Mean characteristics of trees sampled are given in Appendix 11.19;

[t] All intercepts were corrected for bias that occur when converting from logarithmic units (Baskerville 1972); [u] Error mean square;

[v] Mean deviations (%) of predicted from observed = ((Observed - Predicted)*100)/ Observed. The same data set was used for developing equations and calculating deviations;

[w] Includes branchwood and bark.

Table 9.2: The distribution (percent) of dry needle mass in relation to needle age of drained unfertilized black spruce sampled from the vicinity of the ^{15}N experimental plots at bud break in early June 1991 at Wolf Creek, central Alberta[a].

Needle age (yr)						
0[b]	1	2[c]	3	4	5	6+older[d]
20.4[e] (1.68)	13.8 (1.05)	11.4 (0.67)	9.16 (0.71)	6.62 (0.50)	5.48 (0.43)	33.2 (3.10)

[a] Twelve trees representing a range of dbh (1 to 9 cm) were selected and equal number of branches were taken from upper, middle and lower one third crown positions, composited by tree, bagged and stored for three days at 2 - 5 °C. Needles on each branch were separated by needle age, dried at 70 °C for 48 h, equilibrated at room temperature and humidity, needles and branches separated and weighed, and percent contribution of each needle age class to total tree branch needle biomass was calculated.

[b] Needles formed in 1990;

[c] First growing season after ditching.

[d] Six-year-old plus all older needles.

[e] Mean of 12 observations; number in parentheses is the standard error of the mean.

excluding stemwood. In comparison, black spruce foliage, branches and stem bark amounted to 36.6, 23.0 and 4.8% in 1989 and 39.0, 25.0 and 4.8% in 1990 of the total N content, respectively. These components of tamarack contained 8.9, 7.0 and 6.1% in 1989 and 7.1, 4.9 and 1.7% in 1990 of the total fertilizer N taken up by trees, respectively. Corresponding fertilizer N distribution in foliage, branches and stem bark of black spruce were 41.9, 31.4 and 4.5% (1989) and 52, 33.3, and 2.8% (1990), respectively.

Table 9.3: Summary of tree component biomass, nitrogen content, percent nitrogen derived from fertilizer (%NDFF) and recovery of fertilizer nitrogen for tamarack and black spruce fertilized with ^{15}N-labelled urea at the dose of 53 kg $N.ha^{-1}$ at Wolf Creek, central Alberta. Urea applied on 1 June 1989.

Tree	31 August 1989				2 September 1990			
Compt.[b]	Dry wt.	N cont.	NDFF	N recov.[a]	Dry wt.	N cont.	NDFF	N recov.
	---- kg ha^{-1} ----		------ % ------		--- kg ha^{-1} ---		------ % -----	
				Tamarack				
Foliage	595.6	15.36	1.74	0.51	626.9	14.37	2.38	0.65
Branches[c]	2074	12.07	1.76	0.40	2184	12.97	1.85	0.45
Stembark	1665	5.660	3.26	0.35	1753	4.731	1.70	0.15
Stemwood	9227	nd[d]	n d	-	9713	n d	n d	-
Roots	n d	n d	8.56	-	n d	n d	4.96	-
Subtotal	*13562*	*33.09*	-	*1.28*	*14277*	*32.07*	-	*1.25*
				Black spruce				
Foliage[e]								
C	604.2	6.640	6.32	0.79	890.9	10.28	8.74	1.70
C+1	498.6	4.637	3.32	0.29	604.2	5.679	7.87	0.84
C+2	401.0	3.649	2.88	0.20	498.6	4.488	5.08	0.43
C+3+rest	2587	19.38	3.01	1.10	2384.2	19.34	4.46	1.63
Branches[c]	3178	21.54	4.39	1.78	3344.8	25.31	6.37	3.04
Stembark	2046	4.50	3.00	0.25	2153.1	4.952	2.77	0.26
Stemwood	6779	n d	n d	-	7135.5	n d	n d	-
Roots	n d	n d	7.09	-	n d	n d	5.34	-
Subtotal	*16093*	*60.34*	-	*4.42*	*17011.3*	*70.05*	-	*7.90*
Total	***29654***	***93.69***	-	***5.71***	***31286.8***	***102.1***	-	***9.15***

[a] Percent of fertilizer applied.

[b] Component.

[c] May have been overestimated since mean total concentration and %N DFF of needle bearing twigs were used for estimating branch total and fertilizer N content.

[d] nd - not determined.

[e] C- current year, C+1 - one year old. Needle biomass of each age class was estimated using the relationship given in Table 9.2 and tree total needle biomass.

9.3.2 Distribution of nitrogen in understory vegetation

In both years, foliar N concentration of *Betula pumila* (deciduous) was higher than that of other understory species (see Appendix 11.21). However, at a stand level *Ledum groenlandicum* (evergreen) accumulated a slightly higher proportion of fertilizer N in both years relative to *Carex* spp and *B. pumila* (Table 9.4). As observed for trees, %NDFF of foliage was higher than in stems or branches of understory species (see chapter 8). Both the %NDFF and the amount of fertilizer N contained in understory vegetation after four months following fertilizer application averaged 30.5% of the total N contained in aboveground plant biomass and after sixteen months it dropped to 26% (Tables 9.3 and 9.4).

9.3.3 Distribution of nitrogen in soil

A greater proportion of fertilizer N (>50%) applied as urea was retained by the moss and near-surface organic soil. Four months after fertilizer application, about 52% of the applied fertilizer N was recovered within the 0-20 cm depth (Table 9.5). This recovery dropped to 47% twelve months later. The contribution of fertilizer N to total N content was about 0.50% for peat residual in both years and about 0.60% (1989) and 0.52% (1990) for total mineral-N (Table 9.5).

9.3.4. Partial recovery of fertilizer N in the ecosystem

The mean partial recovery of fertilizer N in aboveground tree components was 5.7% four months after fertilizer application, but increased to 9.2% after 16 months (Table 9.6). However, this increase is entirely attributable to black spruce. The amount of fertilizer N recovered in the aboveground components of understory vegetation in 1989 was 8.1% and in 1990 it was 3.9% of the applied fertilizer N. Fertilizer N recovery in soil was about 54.4% in 1989 and 47% 1990. Fertilizer N that volatilized measured during the two weeks immediately

Table 9.4: Summary of understory vegetation aboveground component biomass, nitrogen content, percent nitrogen derived from fertilizer (%NDFF)[a], and recovery of fertilizer nitrogen for tamarack and black spruce on a minerotrophic peatland fertilized with ^{15}N-labelled urea at the dose of 53 kg N.ha^{-1}, at Wolf Creek, central Alberta.

Understory[b]	31 August 1989				2 September 1990		
Component	Dry wt.[c]	N cont.	NDFF	N recov.	N cont.	NDFF	N recov.
	--- kg ha^{-1} ----		------ % ------		kg ha^{-1}	----- % -------	
Carex spp	468.7	9.702	9.32	1.71	6.138	2.72	0.32
Betula pumila							
branches/ stems	1469.0	13.39	7.48	1.89	13.81	3.46	0.90
foliage	231.2	6.048	8.70	0.99	5.762	4.37	0.48
Subtotal	*1700.2*	*19.438*	-	*2.88*	*19.57*	-	*1.38*
Ledum groenlandicum							
branches/ stems	608.9	4.561	15.7	1.35	3.751	13.0	0.92
foliage	275.3	4.620	19.5	1.70	4.063	14.9	1.14
Subtotal	*884.2*	*9.181*	-	*3.05*	*7.814*	-	*2.06*
Others							
branches/ stems	171.0	1.601	6.78	0.21	1.359	2.19	0.06
foliage	60.76	1.255	9.13	0.22	1.120	3.43	0.07
Subtotal	231.76	2.856	-	0.42	2.479	-	0.13
Total	***3284.9***	***41.18***	-	***8.06***	***36.00***	-	***3.88***

[a] Atom abundance of ^{15}N in urea fertilizer was 2.7761.

[b] Assumed no change in aboveground biomass between 1989 and 1990.

[c] Dry wt. - dry weight; N cont. - N content; N recov. - percent of applied fertilizer N recovered.

Table 9.5: Summary of distribution of total N, percent N derived from fertilizer (%NDFF) and fertilizer N recovery for peat residual and mineral-N at Wolf Creek, central Alberta. The ^{15}N-urea was applied on 1 June 1989, at the dose of 53 kg N.ha^{-1}.

Soil	Bulk	31 August 1989			2 September 1990		
depth	density	Total N	NDFF	Recov.[a]	Total N	NDFF	Recov.
cm.	g.m^{-3}	kg ha^{-1}	------ %	------	kg ha^{-1}	------ %	------
				Peat residual			
0-5[b]	0.013	80.31	9.93	15.3	76.15	12.8	18.4
5-10	0.027	239.3	3.36	14.9	231.2	3.73	16.3
10-20	0.078	1319	0.53	15.2	1110	0.54	11.2
20-30	0.135	3496	0.03	1.98	3291	0.00	0.0
Subtotal	-	*5135*	-	*47.4*	*4708*	-	*45.9*
				Mineral N			
0-5	0.013	4.07	26.6	2.04	1.27	17.63	0.42
5-10	0.027	6.07	17.8	2.04	2.69	7.627	0.39
10-20	0.078	21.7	6.34	2.59	12.1	2.398	0.55
20-30	0.135	13.4	1.11	0.28	10.6	0.1304	0.03
30-40	0.160	2.89	0.13	0.01	5.82	0.0425	<0.01
Subtotal	-	*48.1*	-	*6.96*	*32.5*	-	*1.39*
Total	-	***5183***	-	***54.4***	***4741***	-	***47.2***

[a] Percent of applied fertilizer N;

[b] Measured from the surface of live moss;

The recovery of fertilizer N in soil (0-40 cm depth) varied between the two plots in both years, with the higher recovery in plot 1 (data not shown).

Table 9.6: Summary of recovery of fertilizer N on 31 August 1989 and 2 September 1990 at Wolf Creek, central Alberta. The experiment was fertilized on 1 June 1989 at the dose of 53 kg N.ha^{-1}.

Ecosystem component	1989 kg ^{15}N.ha^{-1}	1989 % recovery	1990 kg ^{15}N.ha^{-1}	1990 % recovery
Trees[a]	3.014	5.71	4.847	9.15
Understory vegetation[a]	4.268	8.06	2.055	3.88
Soil	28.81	54.4	25.04	47.2
Volatilization[b]	4.60	8.67	4.60	8.67
Total	***40.7***	***76.8***	***36.5***	***69.0***

[a] Roots not included;

[b] NH_3 volatilization was measured as described in Appendix 11.22.

after urea application amounted to about 8.7% of applied N. The amount of fertilizer retained by the ecosystem (excluding roots) was about 68% (1989) and 60% (1990).

9.4 DISCUSSION

9.4.1 Recovery of fertilizer N in trees

The proportion of N derived from fertilizer was higher in more metabolically active tree tissues, such as current needles and roots, than in older needles and other tissues. These results are in agreement with those obtained for some upland conifers (Mead and Pritchett 1975; Heilman *et al.* 1982; Melin *et al.* 1983; Preston *et al.* 1990).

The amount of fertilizer N recovered (on ha basis) for tamarack did not change over two growing seasons although that of black spruce increased by a relative 78% during the second growing season. Tamarack, a deciduous species, lost its entire foliage biomass (needle litterfall) in 1989. This resulted in a transfer of about 117 g ^{15}N ha^{-1}

(44%) of fertilizer N originally contained in foliage (unit needle litter mass was 0.24 mg needle^{-1}, and needle litter total N concentration and %NDFF were 0.674% and 3.13%, respectively). On the other hand, black spruce may have transferred 6 g $^{15}N.ha^{-1}$ (0.5%) of fertilizer N due to needle litterfall. This is based on the assumption that needle litterfall for black spruce constituted about 5% of the current foliage biomass (obtained by extraporation from data in Table 9.2).

Of the fertilizer N recovered (on ha basis) in aboveground tree components at a stand level, about 82% was recovered in black spruce and 18% in tamarack (Table 9.3). These results may be related to differences in stand density per species (see Table 8.1) and differences in size and strength of sinks for N (see Table 9.3) as discussed below. In order to examine differences in N uptake efficiency between tamarack and black spruce, trees of the same dbh were compared. When this was done fertilizer N uptake for black spruce was 9 (1989) and 13 (1990) times higher than that of tamarack (Fig. 9.1). This may be related to: a) much greater foliage, branch and stembark biomass for black spruce, b) greater sink for N provided by foliage of black spruce, and c) enhanced uptake of N due to possible moderate deficiency of N (Swan 1970) as suggested by total N concentration in current needles of black spruce. On the other hand, the higher foliar N concentration of tamarack may have induced low N uptake. The foliar N status for optimum growth of tamarack has not been established.

There was no determination of N concentration and ^{15}N atom percent excess in stemwood of tamarack and black spruce due to incomplete combustion of samples in the mass spectrometer related to high C:N ratio. This suggests that fertilizer N content of stemwood of either species may have been very low. This is not surprising since insignificant stemwood radial increment was expected at two and three years following lowering of water table by ditching (Dang and Lieffers 1989; Humphrey 1990). This suggests that the stemwood was less metabolically active than other tissues and thus less fertilizer N was allocated to it. My results are in agreement with those of ***Pinus sylvestris*** in Finland (Paavilainen 1973). Contrary to my results, substantial recovery of fertilizer N in stemwood has been reported for conifers that showed significant stemwood growth on well drained

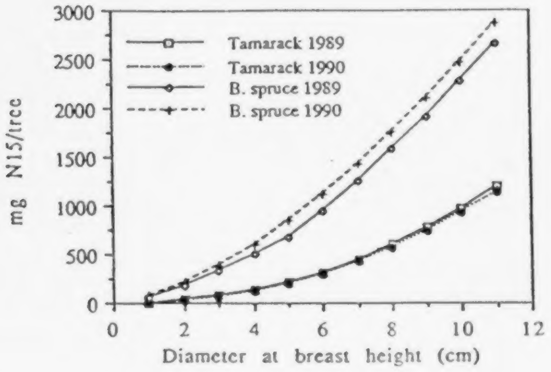

Figure 9.1: The amount of N derived from fertilizer in the aboveground components of tamarack and black spruce in individual trees 13 and 65 weeks following ^{15}N-labelled urea application (1 June 1989) onto a drained minerotrophic peatland at Wolf Creek, central Alberta. For each tree, component biomass was derived using allometric equations (Table 9.1). The amount of N fertilizer for each tree was calculated from total N content and %NDFF of foliage, branches and stembark. The stemwood was not included. Fertilizer N may have been overestimated because total N and %NDFF of needle bearing twigs was used to estimate N in whole tree branches

mineral soil (Mead and Pritchett 1975; Heilman *et al.* 1982; Melin *et al.* 1983; Melin and Nommik 1988; Preston *et al.* 1990).

9.4.2 Recovery of fertilizer N in understory species

Direct comparison of results of different studies on fertilizer N uptake by the understory vegetation is difficult because of differences in variables such as plant species, and overstory vegetation composition and density. In spite of these limitations, general inferences can be made. The trends of recovery of fertilizer in understory vegetation were similar to those reported for upland sites in Sweden (Bjorkman *et al.* 1967; Melin et. al. 1983) and from peatlands in Finland (Paavilainen 1973). To the contrary, Preston *et al.* (1990) observed that the recovery of fertilizer N in understory vegetation on mineral soil sites in British Columbia was less than 3.5%. This may be related to small standing biomass of understory vegetation. My results suggest that understory vegetation in drained peatlands of central Alberta may be a significant sink for applied fertilizer N. The problem may be more serious several years after installation of drainage ditches because I observed dramatic increases in the growth and density of understory species several years after installation of drainage ditches at the Saulteaux River and Goose River Drainage Project sites.

9.4.3 Distribution and recovery of nitrogen in soil

In both years, a high proportion of fertilizer N was recovered within the 0-20 cm soil depth. This is comparable to soil recovery of fertilizer N reported for a *Sphagnum fuscum* open swamp (Paavilainen 1973). The high retention of N originating from NH_4^+-N and urea fertilizer sources has also been reported for live moss (Weber and van Cleve 1981) and organic horizons of upland soils (Nommik 1970; Nommik and Popovic 1971; Overrein 1967, 1970, 1972; Foster *et al.* 1985). Weber and van Cleve (1981) speculated that this indicates tight internal N cyling within the feather moss layer or tying up N in unavailable form. Biochemical reactions may have converted NH_4^+-N initially held on cation exchange sites to become partly non-exchangeable. Additionally, microbial immobilization cannot be ruled out.

The decrease in recovery of fertilizer N for peat residual from the first to the second year suggests net mineralization of N originally immobilized by peat. The decrease in fertilizer mineral-N from 1989 to 1990 may be related to plant uptake, microbial immobilization, and/or retranslocation to unsampled peat depth. My results of a significant measurable amount of fertilizer N as inorganic N near the end of the second growing season following fertilization are in sharp contrast to those reported elsewhere (Nommik and Popovic 1971; Nommik and Moller 1981; Weber and van Cleve 1984; Melin and Nommik 1988). They observed no measurable amounts of fertilizer N as inorganic N in the soil two growing seasons after fertilizer application

The recovery of fertilizer N in soil (0-40 cm) varied between plots in both years, with the higher recovery in plot 1 (results not shown). These results may be related to the slightly higher tree stand density, and a higher proportion of black spruce tree biomass in plot 2 (see chapter 8, Table 8.1) may have resulted in slightly higher fertilizer N uptake. An apparently greater occurrence (observation only) of hummock-hollow micro-relief in plot 2 may have added surface area over the plot's vertically projected area resulting in higher total surface area (Grigal 1985) over which fertilizer N was distributed. Since the recovery of ^{15}N was estimated on the basis of vertically projected area (nominal plot area) instead of total surface area, ^{15}N recovery for the live moss and near-surface soil of plot 2 may have been underestimated more than that of plot 1 was.

9.4.4 Partial budget of fertilizer N in the ecosystem

The relatively low recovery of fertilizer N in aboveground tree components is comparable to results of 11-year-old Scots pine (Nommik 1966; Bjorkman *et al.* 1967) and lodgepole pine (Preston *et al.* 1990). However, recovery of fertilizer N was low compared to conifer studies extending over two growing seasons on mineral soils (Mead and Pritchett 1975; Heilman *et al.* 1982; Melin *et al.* 1983; Melin and Nommik 1988). The low recovery of fertilizer N in peatland tamarack and black spruce trees at Wolf Creek may be related to: a) the high retention of fertilizer N by live moss and near-surface peat, b) the smaller foliar sink for N and initially higher foliar N concentration of tamarack, c) slow growth rate of black spruce resulting in low demand for N, d) loss through NH_3 volatilization as discussed below, and e) the relatively small dose of fertilizer N (53 kg $N.ha^{-1}$). Paavilainen (1972) observed that the growth reaction of trees growing in peatlands can not be efficiently stimulated by a small amount of fertilizer.

Volatilization of NH_3 from soil surfaces increases with higher soil pH (Watkins *et al.* 1972, Ventura and Yoshida 1977), soil surface temperature, air movement over the soil surface (Watkins *et al.* 1972), and with decrease in cation exchange capacity of the soil (Allison 1955). Increased soil moisture enhances volatilization of NH_3 (Ernst and Massey 1960) with greater volatilization of NH_3 occurring in flooded soil (Willis and Sturgis 1944; Ventura and Yoshida 1977). My result is comparable with that reported from mineral soil sites (Melin and Nommik 1988; Nason *et al.* 1988). However, N volatilization at my site was much lower than that reported in the literature (Nommik 1973; Craig and Wollum 1982). The reasons for the low percentage of N loss through volatilization may be that: a) N was applied in solution and this may have enhanced infiltration into the near-surface peat, urea hydrolysis and NH_4^+-N adsorption to cation exchange sites; b) For the 2-week period following urea application, daily mean air temperature ranged from 10 to 19 °C and precipitation totalled 48 mm with the first and large (84%) rainfall event occurring on the ninth day (G.R. Hillman, unpublished data). Thus at that time, most of urea may have been hydrolysed; and c) A presumed high cation exchange capacity of moss and organic soil may have enhanced retention of NH_4^+-N.

My total recovery of fertilizer N in the ecosystem is comparable to that reported for peatlands (Paavilainen 1973) and other ecosystems (Nommik 1966; Heilman *et al.* 1982). The labelled N fertilizer not accounted for in this study during the second growing season averaged 29% of the applied N. This probably included N lost through volatilization during the first growing season, N tied up in plant roots, some translocation of NH_4^+-N, undetermined extractable soluble organic N, and N lost through needle and leaf litterfall as this component was not sampled. At my study site, the amount of fertilizer N tied up in roots probably ranged from 2 to 3%. This estimate is based on the assumption that tree root biomass was similar to that estimated by Lieffers and Rothwell (1987) for tamarack and black spruce wet peatland sites near Saulteaux River, Alberta (55° 10' N; 114° 16' W). My estimate of fertilizer N contained in tree roots is within the range (<2 - 11%) reported for conifer roots (Mead and Pritchett 1975; Melin *et al.* 1983; Melin and Nommik 1988; Preston *et al.* 1983). Underestimation of the surface area contributed by hummock-hollow microrelief (Grigal 1985) may have also resulted in underestimation of mean recovery of ^{15}N.

The results of the present study should be interpreted with caution. Since plots were isolated, some roots of sampled trees that were about 2 m away from the boundary may have been severed during trenching and this may have reduced N uptake. The isotopic tracer method is impaired by an experimental error caused by isotope interchange reactions in soil systems. The interchange between labelled N and the nonlabelled organic soil N dilutes the pool of inorganic N. This results in lower recovery values of fertilizer N for plants and higher ones for soil for NH_4^+ and urea ^{15}N sources, compared with those obtained by the indirect difference method (Melin and Nommik 1988; Preston *et al.* 1990). The high cost of isotopically enriched urea and of analysis of soil and plant samples dictated the use of two replicate plots and the number of trees sampled. This may have compromised the precision of the experiment to some extent.

9.5 CONCLUSIONS

a) As expected, a greater proportion of fertilizer N taken up by trees was allocated to metabolically active components such as foliage, current twigs and roots.

b) Unexpectedly, fertilizer N recovered (on ha basis) in tamarack aboveground components did not change over two years. To the contrary, that of black spruce increased by 79% during the second relative to the first year. That of understory species decreased during the second year.

c) As expected, fertilizer N uptake was greater for black spruce than for tamarack, for trees of the same dbh were compared. This may be related to the bigger N sink (foliage) for black spruce as compared to that of tamarack.

d) Fertilizer N showed little mobility in soil, and tended to accumulate within the 0-20 cm depth. The ability of live moss and near-surface peat to retain $^{15}NH_4^+$-N is related to their high cation exchange capacities, tight internal cycling of N and tying up of N in non-exchangeable form.

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Chapter 10

GENERAL DISCUSSION AND CONCLUSIONS

10.1 INTRODUCTION

My thesis involved silvicultural manipulations (drainage, thinning and NPK fertilization) of forested minerotrophic peatland ecosystems with a goal of altering soil aeration, temperature and water relations of near-surface soil, and nutrient availability and uptake in order to improve tree productivity. To understand how these silvicultural manipulations influence soil nutrients, especially N, and tree productivity, I studied: a) selected physiological processes in the trees, i.e., foliar nutrient accumulation, retranslocation and resorption, carbon fixation and allocation to foliage, and quality of needle litter; and b) uptake efficiency and fate of fertilizer N. This chapter brings together the results reported in chapters 2 through 9 in order to evolve an overall picture of the soil and tree responses. In this chapter general conclusions and silvicultural implications are also drawn and some future research needs for drainage, thinning and fertilization of peatlands for forestry in central Alberta are suggested.

10.2 DRAINAGE, THINNING AND FERTILIZATION

10.2.1 Drainage and thinning

Table 10.1 summarizes responses of soil, understory vegetation and trees to drainage without fertilization. At the Wolf Creek area, drainage resulted in rapid changes in some soil physical properties. Drainage lowered the water table and presumably improved soil water relations, but delayed warming up in spring and cooling in fall of surface soil layers. During summer mean soil temperature was higher on the drained than on the undrained site (G.R. Hillman, unpublished data, see chapter 3). Lowering of water table may have also enhanced aeration of near-surface soil (Campbell 1980). Similar observations have been made in other peatlands in central

Table 10.1: Summary of soil, tree and understory vegetation responses to drainage without fertilization.

Ecosystem component	Response variable	Effect of drainage	Benefit[a]	Chapter
Soil	bulk density	increased	?	3, 4
	excess water	removed	+	3
	aeration	increased	+	3
	temperature	increased	+	3
	nutrient availability	increased	+	3, 4, 5
	water content	decreased	±	2, 3, 4, 5
Trees	- ***Foliage***[b]			
	nutrient concn.	increased	+	3, 4, 5, 6
	nutrient patterns	changed	+	6
	NA	increased	+	5
	g_m	improved	+	5
	g_s	nil	0	5
	unit needle mass			
	- tamarack	nil	?	3, 4, 6
	- black spruce	decreased	?	3, 4, 6
	- ***Stemwood increment***			
	- tamarack	increased?	+	inferred
	- black spruce	nil	0	from results
	- ***Root biomass***	increased?	+	chapter 3
	- ***Needle litter***			
	- nutrients			
	concentration	increased	±	7
	N resorption	decreased	-	7
	UE[c]	decreased	-	7
	- unit needle mass	nil	0	7
Understory vegetation				
	- species composition	changed?	?	Field
	- stand biomass	increased	-	observations
	- competition	increased	-	at SR and FTM[d]

[a] Effect on tree growth: ? - unknown; + - positive effect; - - negative effect; ± - both positive and negative effects; 0 - no effect;

[b] NA - net assimilation rate; g_m - mesophyll conductance to CO_2; g_s - stomatal conductance to H_2O (measure of plant water relations);

[c] UE - use efficiency;

[d] Saulteaux River (central Alberta) and Fort McMurray (north central Alberta) Drainage Projects.

Alberta (Lieffers and Rothwell 1986, 1987). At Wolf Creek, the bulk density of drained near-surface peat was higher than that of the undrained site.

One of the objectives was to examine drainage effects on foliar nutrient concentrations and contents, photosynthesis and needle mass. This study revealed that drainage increased foliar nutrients for both tamarack and black spruce. However, drainage alone did not alleviate nutrient deficiencies that existed before ditching for both tree species (chapters 3 and 4). Similar results have been reported from central Alberta (Humphrey 1990; Lieffers and Macdonald 1990). Improved soil conditions and foliar nutrient status also enhanced ecophysiological performance by increasing rates of net assimilation (NA) and mesophyll conductance (g_m) of tamarack and black spruce. However, tree water relations (g_s) were not affected (chapter 5). In natural peatlands conifers have a small shallow root system, since I measured water relations two and three years following ditching the trees may not have had sufficient time for full adjustment of the root system to the new water table level.

Drainage also delayed bud break and needle senescence (chapters 3, 6 and 7). On the drained site, this may be related to delayed warm-up and cooling of surface soil layers in spring and fall, respectively. Drainage did not change seasonal nutrient patterns although it increased foliar N, P and K concentrations, contents and fluxes in current needles of both species during the growing season (chapter 6). These are indicative of changes in demand due to increased tree growth as well as increased availability and uptake of nutrients. The question is how did these changes in soil environment, foliar nutrients and ecophysiology affect tree photosynthate allocation? In this study, photosynthate allocation to roots, stem- and branch-wood was not measured. Thus, the following discussion is incomplete because it is based on ecophysiology, foliar nutrient and unit needle mass response results, and inferred soil fertility.

For black spruce, unit needle mass decreased but NA increased as drainage responses (chapters 3 and 5). This may be related to an increased proportion of photosynthate allocation to belowground related to: a) expansion of the root system to take advantage of a deeper, more aerated profile; b) initially unfavorable high foliage/root mass ratio of black spruce; and c) limited soil availability of N. There is evidence that plants produce a high root/shoot ratio under N stress (Davidson 1969; Ericsson 1981; Linder and Axelsson 1982).

In contrast to black spruce, unit needle mass of tamarack was unaffected (1989) or was increased (1990) by drainage (chapters 3, 4 and 6) presumably due to: a) more favorable foliage/root mass ratio prior to ditching, and b) less dependence of tamarack on uptake of soil mineral-N for current growth (chapters 8 and 9). This is supported by much higher fertilizer N uptake by black spruce as compared to that of tamarack (see chapters 8 and 9). N requirement for tamarack is largely met through more efficient internal cycling and resorption before needle abscission (chapter 7). I hypothesize that, soon after lowering of water table, allocation of photosynthate to belowground for tamarack is not as important as it is for black spruce. Because tamarack does not rely heavily on soil N for current growth, thus increased allocation to the root system is less important than for black spruce.

The preferential allocation of carbon to roots as inferred from reduced unit needle mass of drained black spruce helps to explain the previously documented delay of 3 - 6 years in radial increment response of black spruce to drainage (Dang and Lieffers 1989; Humphrey 1990). There have been no studies on tamarack stemwood radial increment in recently drained peatlands. Because it is not as important for tamarack to allocate resources preferentially to belowground, I hypothesize that there will be immediate stemwood radial increment response of drained tamarack.

Drainage increased the concentrations and contents of N and P in needle litter on the drained site (chapter 7) which could be beneficial to tamarack and black spruce growth since both respond to fertilization. Similar beneficial effects in mixtures of Sitka spruce and hybrid larch were attributed to greater N release through rapid decomposition and mineralization of larch litter as compared to spruce litter (Caryle and Malcom 1986).

Thinning improved the nutrition of drained black spruce as revealed by increased foliar N content, and P concentration and content (chapter 2). This was likely due to: a) reduced between-tree competition for small pools of available N and P; b) nutrient input from decomposition of thinning slash (Miller *et al.* 1976; Ingestad *et al.* 1981); c) increased decomposition as a result of higher soil temperature; d) adequate moisture in upper peat layers may have increased ion mobility and transpiration rates and so increased nutrient uptake; e) higher retranslocation of N and P from older needles in response to faster growth of current needles, and f) improved root development of residual trees. Increased foliar nutrient status of residual trees in thinned stands resulted in an increase in unit needle mass of current needles. As for drainage, thinning did not alleviate sub-optimal foliar nutrient concentrations that existed before thinning (chapter 2).

10.2.2 Fertilization

The hypothesis tested was that fertilization increases foliar nutrients, photosynthesis and unit needle mass of tamarack and black spruce. Table 10.2 summarizes responses to fertilization of undrained and recently drained peatlands. The chances of improving tree growth through NPK fertilization of the undrained site are limited. This is because fertilization did not increase foliar N, P and K concentrations and contents as much as it did on the drained site (chapters 3, 5 and 6). It appears that low foliar nutrient status of trees following fertilization of the undrained site resulted from reduced uptake (Shoulders and Ralston 1975; Glinski and Stepniewski 1985) and transport from roots to leaves related to low transpiration (Smith *et al.* 1989) due to poor aeration. Moreover, the death of some black spruce in high N dosage plots on the undrained site during the second growing season suggests ammoniacal toxicity.

My studies of tree nutrition and growth in relation to drainage-fertilization at Wolf Creek, and thinning-fertilization at Goose River suggest that N is the most limiting mineral nutrient (chapters 2, 3, 4, 5 and 6). This is supported by an increase in foliar N concentration and unit needle mass of both species on N fertilized plots. However, at Wolf Creek urea fertilization resulted in apparent imbalances of other foliar nutrients (chapter 4) and decreased photosynthesis on both sites

Table 10.2: Summary of tree responses to phosphorus, potassium and urea fertilization of undrained and recently drained minerotrophic peatland sites at Wolf Creek, central Alberta.

Tree response variable	Tamarack		Black spruce		
	Response	Benefit	Response	Benefit[a]	Chapter
Unfertilized vs N_0PK fertilized[d]					
Foliage[b]					
N concn.	nil	0	nil	0	2, 3, 5, 6
P and K concn.	increased	+	increased	+	2, 3, 5, 6
Other nutrient concentration	decreased	-	diluted	-	4
NA	increased	+	increased	+	5
gm	increased	+	increased	+	5
gs	nil	0	nil	0	5
unit needle mass	nil	0	nil	0	3, 4, 6
Stem biomass	?	?	?	?	
Root biomass	?	?	?	?	
Needle litter					
N concn.	nil	0	nil	-	7
P and K concn.	increased	±	increased	±	7
N resorption	nil	0	?	?	7
P and K resorption	increased	±	?	?	7
N UE	nil	-	nil	-	7
P and K UE[c]	decreased	-	decreased	-	7
unit needle mass	nil	0	nil	0	7
Undrained-N_0PK vs undrained-NPK fertilized					
Foliage					
N concn.	increased	+	increased	+	2, 3, 5, 6
P and K concn.	decreased	-	diluted	-	2, 3, 5, 6
Other nutrient concentration	decreased	-	diluted	-	4
NA	decreased	?	decreased	?	5
gm	increased	+	nil	0	5
gs	nil	0	nil	0	5
unit needle mass	increased	+	nil (1989)	0	3, 4, 6
			decreased (1990)	?	3, 4, 6
Stem biomass	?	?	?	?	
Root biomass	?	?	?	?	

[a,b,c] as in table 10.1

[d] Generalization for undrained and drained sites.

Table 10.2: Continued.

Tree response variable[a]	Tamarack		Black spruce		
	response	Benefit	Response	Benefit	Chapter
Undrained-N_0PK vs undrained-NPK fertilized					
Needle litter					
N concn.	increased	-	increased	-	7
P and K concn.	decreased	+	nil	0	7
N resorption	decreased	-	?	?	7
P and K resorption	increased	-	?	?	7
N UE	decreased	+	decreased	+	7
P and K UE	increased	+	increased	+	7
unit needle mass	increased	?	nil	0	7
Drained-N_0PK vs drained-NPK fertilized					
Foliage					
N concn.	increased	+	increased	+	3, 5
P and K concn.	decreased	-	diluted	-	3, 5
Other nutrient	decreased	-	diluted	-	3, 4, 5
NA	decreased	-	decreased	?	5
gm	decreased	-	decreased	?	5
gs	decreased	-	nil	?	5
unit needle mass	increased	+	increased	+	3, 4, 5
Stem biomass	?	?	?	?	
Root biomass	?	?	?	?	
Needle litter					7
N concn.	increased	-	nil	0	7
P and K concn.	decreased	+	nil	0	7
N resorption	decreased	-	?	?	7
P and K resorp.	increased	+	?	?	7
N UE[b]	decreased	-	decreased	-	7
P and K UE	increased	+	increased	+	7
unit needle mass	increased	+	nil	?	7

(chapter 5). Increased unit needle mass of drained N-fertilized tamarack and black spruce (chapters 3, 4 and 6) could indicate an increase in allocation to both above- and belowground. Alternatively, increased unit needle mass could indicate preferential allocation of photosynthate to aboveground in response to increased N availability. This is in agreement with the results of carbon allocation when N stressed *Salix* clones (Erricson 1981) and *Pinus sylvestris* (Linder and Axelsson 1982) were N fertilized. My results suggest that the previously documented delay of 3 - 6 years in radial increment response of black spruce to peatland drainage (Dang and Lieffers 1989; Humphrey 1990) could likely be reduced by N fertilization. For tamarack, N fertilization may result in greater stemwood radial increment than in unfertilized trees (not measured).

My results suggest that N fertilization of drained minerotrophic peatlands in central Alberta may be necessary in order to increase tree productivity. The ^{15}N-labelled urea fertilizer experiment provided insight into tree fertilizer N uptake, distribution and soil chemistry. The ^{15}N-labelled urea fertilizer study revealed that fertilizer N uptake during the first two years after fertilizer application was much greater for black spruce as compared to tamarack (chapters 8 and 9). This suggests that tamarack is less reliant on soil mineral-N for N requirements. The study also revealed that of the fertilizer N applied 47% was immobilized in surface layers of peat, about 9.2% was taken up by trees and 4-8% was recovered in understory vegetation. The low N-fertilizer uptake by trees may be in part due to: a) slow growth of trees (small sink size and strength); b) low N dose used resulted in relatively low concentration of fertilizer mineral-N that was available for tree uptake; and c) late fertilizer application. My results seem to suggest that dosage of N fertilizer and timing of N fertilizer application in relation to bud break may be critical if growth of tamarack and black spruce tree is to be improved. My results also suggest that understory vegetation species compete with trees for applied N because a significant amount of ^{15}N was recovered in understory. However, ^{15}N taken up by deciduous understory vegetation will recycle through litter fall and may be available to trees as litter decomposes.

The ^{15}N fertilizer study also showed that foliar ^{15}N content decreased with needle age suggesting preferential allocation of fertilizer N to more actively growing tissues (chapters 8 and 9). However, my study did not show the continuous cycling of N from older to new tissues since ^{15}N content of older needles and branches did not change during the second growing season. This does not necessarily mean that there was no cycling of N from older to new tissues.

Sampling of tree components during the second growing season following fertilizer application did not coincide with periods of retranslocation of N from older to new tissues, i.e., during bud break, or stem, branch and root growth.

10.3 PEATLAND ECOSYSTEM UTILIZATION - PRACTICAL IMPLICATIONS

Increasing the productivity of trees in undrained peatlands through fertilization is not silviculturally viable because: a) fertilizer uptake and tree growth response are limited by other factors related to water saturation, and b) foliar responses are short lived (foliar N and P of tamarack and black spruce decreased significantly during the third growing season following fertilization) (A.G. Mugasha, unpublished data).

Drainage of minerotrophic peatlands increases nutrient availability and uptake. However, my study showed that drainage without fertilization did not alleviate sub-optimal foliar levels of N and P and of some micronutrients that existed before ditching, especially for black spruce. Since tamarack appears not to rely heavily on uptake of soil mineral-N, it is likely that reasonable stemwood growth can be realised without fertilization. However, fertilization may be necessary for successful growth of black spruce in drained minerotrophic peatlands.

Drainage alone or with fertilization improved the needle litter nutrient quality of tamarack. This may increase overall nutrient availability in the forest through tamarack litterfall and decomposition. These results suggest that management of mixed stands of black spruce and tamarack may be beneficial since both species respond to increased N availability. However, research is required to determine: a) if black spruce will benefit from growing in mixed plantations, and b) the appropriate mixture that would result in optimum growth of black spruce.

After six years (Saulteaux River) and eleven years (Fort McMurray) following ditching of minerotrophic peatlands, the drained sites were invaded by dense understory vegetation (A.G.Mugasha, field observations). This vegetation competes for limited nutrient pools and could reduce the growth potential of trees. Control of understory vegetation should be considered in order to optimally improve tree growth. On the other hand, dense growth of understory vegetation following ditching of minerotrophic peatlands may be beneficial to wildlife since browse and forage quality may be enhanced.

These short-term (2 yr) positive responses to drainage, thinning and NPK fertilization are good signs to forest managers interested in intensive management of forested minerotrophic peatlands. However, a cost-benefit analysis of these silvicultural manipulations cannot be done until we know how these foliar responses translate into stemwood increment. It is anticipated that the effect of drainage (Dang and Lieffers 1989; Humphrey 1990), and thinning would last for a longer period. This is because thinning results in increased needle mass (increased sink size and strength for N) and takes several years for crown to close. On the other hand, the effect of N and P fertilization would probably last for a short period.

N fertilization of drained peatlands may result in other benefits or problems. N fertilization decreased production of defensive chemicals for trembling aspen and hence increased insect defoliation (Bryant *et al.* 1987). On the other hand, increased resistance to insect attack with N fertilization has been reported for several conifers (Waring and Pitman 1985; Cates *et al.* 1987). Fertilizers leached from soil may enter streams and end up in rivers and/or lakes where they may result in eutrophication and/or health hazards to humans, wildlife or fish populations (see Stockner and Shortreed 1978; Heatherington 1985; Turchenek 1990).

10.4 SOME FUTURE RESEARCH NEEDS

a) Long term changes in availability of nutrients, particularly N and P, and tree uptake in drained unfertilized minerotrophic peatlands need to be investigated, so that nutrient requirements and fertilization needs can be assessed.

b) Both drainage and thinning increased foliar nutrient concentrations and needle mass. Quantitative information is required on the effect of these treatments on nutrient availability. More emphasis should be placed on the interaction of thinning and fertilization treatments on soil temperature and soil moisture and how they affect availability and uptake of nutrients.

c) Drainage and fertilization improved needle litter quality of tamarack. There is a need to investigate nutrient recycling through needle litterfall and its contribution to plant nutrient availability.

d) Urea and ammonium nitrate are the two N fertilizers used commonly in forest fertilization and the response to each is related to soil characteristics, species of trees and weather conditions following fertilization (Harrington and Wierman 1990). Research is required to determine the suitable source and optimum level of N fertilizer for unthinned and thinned tamarack and black spruce stands on drained minerotrophic peatlands.

e) More work is required to investigate how drainage with or without fertilization influences carbon allocation to above- and belowground tree portions.

f) Nitrogen fertilization may have resulted in imbalances in foliar nutrient concentrations and this may have caused growth disturbances. Quantitative data are needed on the effect of applying balanced fertilizers in drained minerotrophic peatlands on: a) foliar and ecophysiological responses of tamarack and black spruce, and b) carbon allocation to above- and below-ground tree components.

g) More research is also required to investigate stemwood growth that may eventually occur in drained and fertilized minerotrophic peatlands. Information is required on the time it takes to get significant stemwood increment, and on the duration and magnitude of stemwood response.

h) Long-term retention of photosynthetically-active needles increases the carbon return per unit of invested nutrient for black spruce in nutrient stressed sites (Small 1972). Increased nutrient availability may modify this adaptation. Thus, research is required to investigate the effect of increased nutrient availability on leaf turnover rate for black spruce.

i) The results of my studies are applicable to shallow minerotrophic peatlands. However, there are many different types of peatlands in western Canada. Research is required to investigate effects of drainage and fertilization on nutrient dynamics and tree growth in different forested peatland types.

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Chapter 11

APPENDICES

Appendix 11.1: Summary of peat thickness (cm) of the experimental black spruce area at Goose River, central Alberta.

Thinning treatment	Block number			
	1	2	3	4
Thinned plots	F1[1] 38(11)[2]	F2 58(8)	F0 36(10)	F2 55(22)
	F5 31(14)	F3 34(10)	F2 45(24)	F3 43(13)
	F6 45(11)	F5 29(27)	F3 38(15)	F5 66(10)
	F7 40(14)	F7 44(25)	F7 38(13)	F6 43(28)
Sub mean	39 (18)	41(31)	35(17)	51(25)
Unthinned plots	F2 56(10)	F0 43(22)	F0 37(11)	F4 39(12)
	F3 28(10)	F1 40(9)	F2 33(30)	F5 41(14)
	F5 46(24)	F5 55(20)	F4 33(20)	F6 45(6)
	F7 40(19)	F7 43(10)	F7 37(7)	F7 48(22)
Sub mean	42 (29)	(45(22)	39(19)	43(17)
Overall mean	40 (25)	43(26)	37(19)	47 (23)

[1] Randomly selected fertilization treatment plots as defined in Fig. 2.1.

[2] Mean peat depth (cm), with coefficient of variation (%) in parenthesis. Number of observations was 6.

Appendix 11.2: Summary of particle size distribution and textural class for mineral soil horizons of the experimental black spruce area at Goose River, central Alberta.

Location of profile	Horizon[1]	Particle size distribution Clay	Silt	Sand	Soil texture class
		%			
Block 1	Ahejg	31.3	46.6	22.1	Clay loam
	Aeg	25.5	41.0	33.5	Loam
	IIBtg	31.7	21.1	47.2	Sandy clay loam
	IICg	33.7	36.2	30.1	Clay loam
Blocks 1 & 2	Ahg	17.0	28.7	54.3	Silt loam
	Aeg	37.0	27.6	35.4	Clay loam
	IIBtg	41.2	27.5	31.3	Clay
	IICg	18.9	38.3	42.8	Loam
Block 4	Aheg	37.9	51.4	10.7	Silty clay loam

[1] For horizon thickness see Appendix 11.3.

[2] Particle size distribution was determined by the hydrometer method on soil ground to pass a 2 mm mesh sieve followed by oxidation of organic matter with hydrogen peroxide (McKeague 1978).

Appendix 11.3: Soil profile descriptions of the thinning-fertilization experimental area at Goose River, Central alberta.

Appendix 11.3.1: Description of soil profile 1 located in block 1 in the thinning-fertilization experiment.

Horizon	Depth cm	Description
Of_1	0 - 15	Brown (7.5YR 4/6 m, unrubbed), bright brown (7.5YR 5/6 m, rubbed); abundant, medium and coarse roots; smooth boundary; Von Post scale of decomposition = 3
Of_2	15 - 30	Very dark brown (7.5YR m, unrubbed), brownish black (7.5YR m, rubbed), abundant, medium and coarse roots; abrupt boundary; Von Post scale of decomposition = 3
Of_3	30 - 40	Black (7.5 YR 1.7/1 m, unrubbed), Black (10YR 1.7/1 m, rubbed); fine to very fine roots, abrupt boundary; von Post scale of decomposition = 4
Ahejg	40 - 45	Black (10YR 1.7/1 m); sandy clay loam; weak, coarse platy, plentiful, fine to very fine roots; no carbonates, no coarse fragments; clear smooth boundary.
Aeg	45 - 58	Brown (10YR 4/4 m), dark grayish yellow matrix (2.5Y 5/2 m); loam; weak, coarse platy; plentiful, fine to very fine roots; no carbonates, no coarse fragments; clear smooth boundary.
AB	58 - 65	Transition horizon; few, very fine roots; clear smooth boundary.
IIBtg	65 - 86	Yellowish brown (10YR 5/4 m), grayish olive matrix (5Y 5/2 m); sandy clay loam; moderate, very fine angular blocky; few coarse fragments; no roots; gradual smooth boundary.
IICg	86 +	Abundant brown mottles (10YR 4/4 m), gray matrix (5Y 5/1 m) ; clay loam; massive; charcoal inclusions; few gravel sized fragments, no carbonates.

Appendix 11.3.2: Description of soil profile 2 located in block 2 treatment T1 of the thinning-fertilization experiment.

Horizon	Depth	Description
	cm	
Of_1	0 - 25	Dark brown (7.5YR 3/4 m, unrubbed), dull brown (7.5YR 5/4 m, rubbed); abundant, medium to fine, random roots; clear smooth boundary; Von Post scale of decomposition = 3
Of_2	25 - 40	Black (7.5YR 2/1m, unrubbed), brownish black (7.5YR 2/2m, rubbed), abundant, medium to coarse, random roots; clear smooth boundary; Von Post scale of decomposition = 4.
Ahg	40 - 45	Black (7.5Y 2/1 m); sandy loam; weak medium angular blocky; few, fine vertical roots; no coarse fragments; no carbonates; abrupt wavy boundary.
Aeg	45 - 65	Abundant dull yellowish brown mottles (10YR 5/4 m), yellowish brown matrix (2.5Y 4/2 m); clay loam; weak, medium platy; few fine vertical roots; abrupt smooth boundary.
AB	58 - 65	Transition horizon
IIBtg	65 - 95	Abundant brownish mottles (10YR 4/4 m), dark grayish yellow matrix (2.5Y 4/2 m); clay; weak, very fine angular blocky; no coarse fragments; no carbonates; few very fine vertical roots; clear smooth boundary.
BC	95 - 105	Transition horizon; no roots; clear smooth boundary.
IICg	105 +	Abundant brown mottles (10YR 4/4 m), gray matrix (5Y 5/1 m); loam; massive; ; charcoal inclusions (3 cm in diameter); few gravel sized fragments.

Appendix 11.3.3: Description of soil profile 3 located in block 3 treatment To of the thinning-fertilization experiment.

Horizon	Depth	Description
	cm	
Of_1	0 - 25	Brown (7.5YR 4/4 m, unrubbed), dull brown (7.5YR 5/6 m, rubbed); abundant, very fine random roots; clear smooth boundary; Von Post scale of decomposition = 2
Of_2	25 - 47	Brownish black (7.5YR 2/2m, unrubbed), darkish brown (7.5YR 3/3 m, rubbed); abundant, fine, random roots; abrupt smooth boundary; Von Post scale of decomposition = 3
Ahg	47 - 63 +	Black (7.5 YR 2/1 m); silty clay loam; weak, fine subangular blocky; few fine to coarse roots; clear smooth boundary.

Appendix 11.4: ANOVA summary of planned contrasts for fertilization treatments within stand density and distance factors for absolute values of foliar nitrogen, phosphorus, potassium and unit needle mass response variables of black spruce at Goose River, central Alberta.

			Stand density			Distance	
			Unthin vs. thin			Prox. vs Dist	
Foliar response	Fertilization level[1]	Fig.	t-value	P>t	Fig.	t-value	P>t
N concn.	N	2.4a	2.43	0.015	2.5a	2.40	0.020
	NP		-0.849	0.40		1.41	0.16
	NK		0.283	0.78		1.41	0.16
	NPK		-0.141	0.89		0.849	0.40
N cont.	N		2.31	0.026		-1.04	0.30
	NP		-1.83	0.074		1.62	0.11
	NK		2.27	0.029		0.00	1.00
	NPK		1.59	0.12		5.06	<0.001
Needle mass	N		3.10	0.003		-1.38	0.17
	NP		-1.51	0.14		-0.554	0.58
	NK		2.95	0.005		-1.75	0.086
	NPK		2.42	0.002		3.51	0.001
P concn.	P	2.4b	0.845	0.40	2.5b	1.10	0.28
	NP		-1.69	0.098		0.00	1.00
	PK		2.54	0.015		2.20	0.033
	NPK		-0.845	0.40		1.10	0.28
P cont.	P		1.00	0.32		0.358	0.72
	NP		-2.35	0.024		-0.537	0.59
	PK		4.08	<0.001		4.70	<0.001
	NPK		0.800	0.43		3.18	0.003
Needle mass	P		0.529	0.60		-0.185	0.85
	NP		-1.51	0.14		-0.554	0.58
	PK		2.65	0.011		0.185	0.85
	NPK		2.42	0.020		3.51	0.001
K concn.	K	2.4c	0.496	0.62	2.5c	0.258	0.80
	PK		0.248	0.81		1.29	0.20
	NK		-0.248	0.81		0.258	0.80
	NPK		-1.74	0.090		0.775	0.44
K cont.	K		1.31	0.20		0.667	0.51
	PK		2.00	0.052		1.08	0.28
	NK		1.31	0.20		-0.500	0.62
	NPK		-0.345	0.73		2.83	0.007
Needle mass	K		1.36	0.18		0.738	0.46
	PK		2.65	0.011		0.185	0.85
	NK		2.95	0.005		-1.75	0.086
	NPK		2.41	0.020		3.51	0.001

[1] Degree of freedom for each contrast was 1. Error mean square and corresponding degrees of freedom for each response variable are given in Table 2.3.

Appendix 11.5: ANOVA summary of planned contrasts for fertilization treatments within stand density and distance factors for foliar nitrogen and unit needle mass response variables of black spruce at Goose River, central Alberta.

			Response variable					
			N concentration		N content		Needle mass	
Fig.	Treatment	Contrasts[1]	t-value	P>t	t-value	P>t	t-value	P>t
2.4a	Unthin	N vs NP	1.35	0.19	4.95	<0.001	7.57	<0.001
		N vs NK	1.63	0.12	0.055	0.96	0.198	0.87
		N vs NPK	1.00	0.33	3.62	0.002	6.28	<0.001
		NP, NK vs NPK	-0.516	0.58	1.29	0.21	2.76	0.002
		N,P,K vs NPK	3.70	0.001	8.27	<0.001	8.61	<0.001
		Error MS[2]	0.040		29.9		0.080	
2.4a	Thin	N vs NP	-2.67	0.014	1.35	0.19	3.78	<0.001
		N vs NK	-0.27	0.79	0.070	0.95	0.163	0.87
		N vs NPK	-2.39	0.026	3.58	0.002	6.56	<0.001
		NP, NK vs NPK	-1.07	0.30	3.31	0.003	5.29	<0.001
		N,P,K vs NPK	5.35	<0.001	8.32	<0.001	10.9	<0.001
		Error MS	0.0064		20.7		0.060	
2.5a	Proxi.	N vs NP	0.589	0.56	3.75	0.001	6.92	<0.001
		N vs NK	1.34	0.20	-0.495	0.63	0.17	0.87
		N vs NPK	0.739	0.47	2.87	0.009	5.55	<0.001
		NP, NK vs NPK	0.260	0.80	1.44	0.17	2.32	0.031
		N,P,K vs NPK	3.08	0.006	10.9	<0.001	10.2	<0.001
		Error MS	0.030		10.2		0.040	
2.5a	Distant	N vs NP	-0.300	0.77	4.42	<0.001	5.74	<0.001
		N vs NK	0.880	0.39	0.468	0.65	0.007	0.99
		N vs NPK	-1.02	0.32	5.60	<0.001	7.83	<0.001
		NP, NK vs NPK	-1.51	0.15	3.65	0.002	5.72	<0.001
		N,P,K vs NPK	6.44	<0.001	11.6	<0.001	10.8	<0.001
		Error MS	0.010		23.1		0.080	

[1] Degrees of freedom for each contrast and for each error term for stand density and distance levels were 1, 21 and 24 respectively.

[2] MS - mean square.

Appendix 11.6: ANOVA summary of planned contrasts for fertilization treatments within stand density and distance factors for foliar phosphorus and unit needle mass response variables of black spruce at Goose River, central Alberta.

			Response variable					
			P concentration		P content		Needle mass	
Fig.	Treatment	Contrasts[1]	t-value	P>t	t-value	P>t	t-value	P>t
2.4b	Unthin	P vs NP	-7.16	0.001	-0.628	0.54	8.20	<0.001
		P vs PK	-0.597	0.56	-0.683	0.50	-0.566	0.58
		P vs NPK	-7.24	<0.001	-1.64	0.12	6.93	<0.001
		NP, NK vs NPK	-3.88	0.001	-1.13	0.27	3.59	0.002
		N,P,K vs NPK	0.426	0.67	4.30	<0.001	8.60	<0.001
		Error MS[2]	0.0007		0.840		0.080	
2.4b	Thin	P vs NP	-12.7	<0.001	-4.90	<0.001	7.27	<0.001
		P vs PK	1.20	0.24	2.75	0.012	1.63	0.12
		P vs NPK	-11.7	<0.001	-2.49	0.021	10.0	<0.001
		PK, NK vs NPK	-6.89	<0.001	-1.63	0.12	6.46	<0.001
		N,P,K vs NPK	-37.5	<0.001	5.17	<0.001	10.9	<0.001
		Error MS	0.0004		0.440		0.060	
2.5b	Proxi.	P vs NP	-10.2	<0.001	-3.00	0.007	10.5	<0.001
		P vs PK	-1.50	0.15	-0.651	0.52	0.500	0.62
		P vs NPK	-10.0	<0.001	-3.87	0.001	9.10	<0.001
		PK, NK vs NPK	-4.81	<0.001	-2.36	0.028	4.16	<0.001
		N,P,K vs NPK	-0.84	0.41	4.71	<0.001	10.2	<0.001
		Error MS	0.0005		0.330		0.040	
2.5b	Distant	P vs NP	-7.21	<0.001	2.32	0.031	7.14	<0.001
		P vs PK	1.27	0.22	1.74	0.096	0.636	0.53
		P vs NPK	-6.70	<0.001	-1.02	0.32	9.26	<0.001
		PK, NK vs NPK	-4.31	<0.001	-0.84	0.41	6.21	<0.001
		N,P,K vs NPK	-0.077	0.94	5.15	<0.001	10.8	<0.001
		Error MS	<0.001		0.82		0.08	

[1] Degrees of freedom for each contrast and for each error term for stand density and distance levels were 1, 21 and 24 respectively;

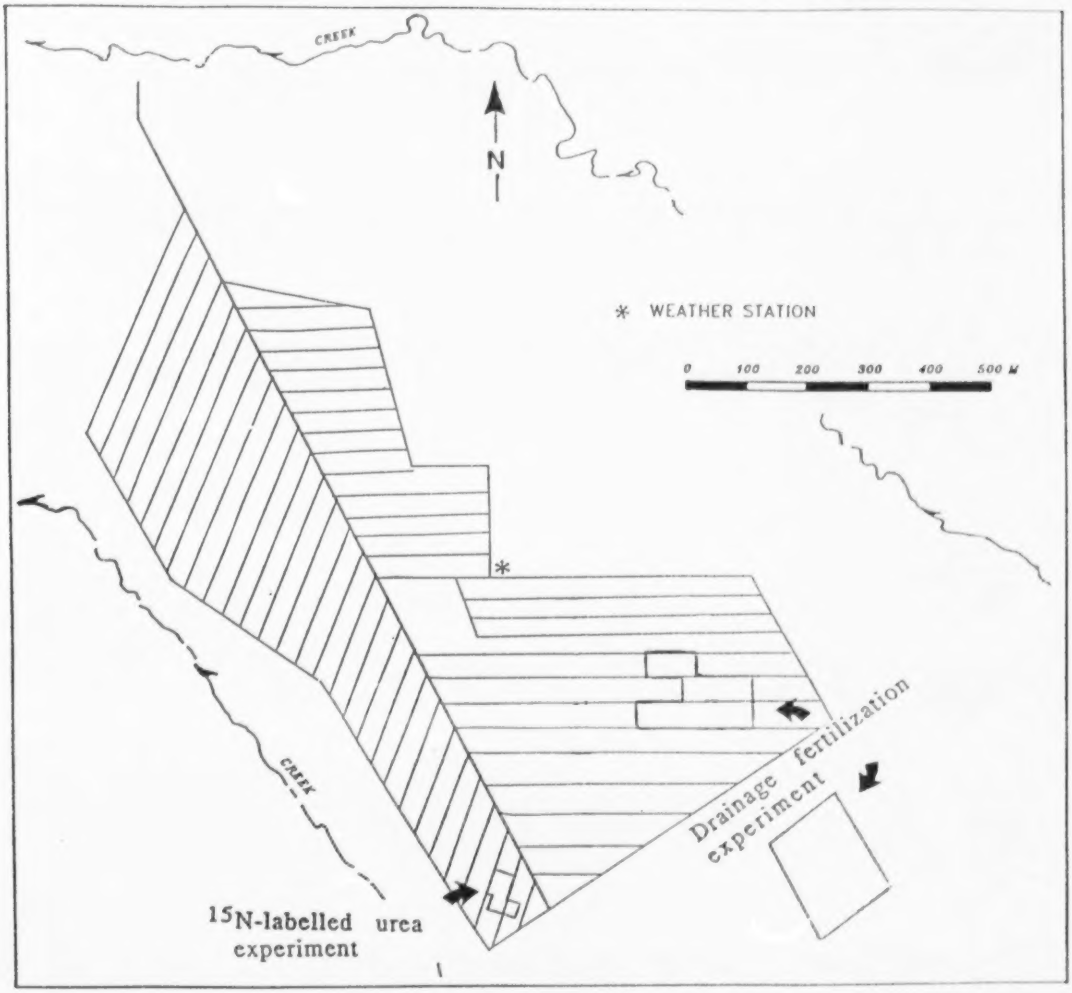
[2] MS - mean square.

Appendix 11.7: ANOVA summary of planned contrasts for fertilization treatments within stand density and distance factors for absolute values of foliar potassium and unit needle mass response variables of black spruce at Goose River, central Alberta.

			Response variable					
			K concentration		K content		Needle mass	
Fig.	Treatment	Contrasts[1]	t-value	P>t	t-value	P>t	t-value	P>t
2.4c	Unthin	K vs PK	1.49	0.15	1.13	0.27	0.354	0.73
		K vs NK	-3.43	0.003	-0.947	0.36	1.77	0.092
		K vs NPK	-1.69	0.11	3.95	0.001	7.85	<0.001
		PK, NK vs NPK	-0.831	0.42	4.45	<0.001	7.84	<0.001
		N,P,K vs NPK	-0.324	0.75	5.20	<0.001	8.60	<0.001
		Error MS[2]	0.0065		9.13		0.080	
	Thin	K vs PK	1.11	0.28	1.98	0.061	1.80	0.087
2.4c		K vs NK	-4.29	<0.001	-1.05	0.31	3.76	0.001
		K vs NPK	-4.29	<0.001	2.55	0.019	10.2	<0.001
		PK, NK vs NPK	-3.12	0.005	2.40	0.026	6.45	<0.001
		N,P,K vs NPK	-3.88	0.001	3.35	0.003	10.9	<0.001
		Error MS	0.0066		7.64		0.060	
2.5c	Proxi.	K vs PK	1.11	0.28	1.98	0.062	1.60	0.12
		K vs NK	-4.98	<0.001	-0.72	0.48	4.80	<0.001
		K vs NPK	-4.06	0.001	3.34	0.003	10.2	<0.001
		PK, NK vs NPK	-2.45	0.023	3.12	0.005	8.60	<0.001
		N,P,K vs NPK	-3.52	0.002	3.68	0.001	10.2	<0.001
		Error MS	0.0040		4.06		0.040	
2.5c	Distant	K vs PK	1.71	0.10	31.5	0.15	0.707	0.49
		K vs NK	-3.75	0.001	-1.30	0.21	1.49	0.15
		K vs NPK	-2.54	0.019	3.74	0.001	9.33	<0.001
		PK, NK vs NPK	-1.75	0.096	4.19	<0.001	8.63	<0.001
		N,P,K vs NPK	-1.14	0.27	5.34	<0.001	10.8	<0.001
		Error MS	0.0067		10.8		0.08	

[1] Degrees of freedom for each contrast and for each error term for stand density and distance levels were 1, 21 and 24 respectively.

[2] MS - mean square.


CREEK
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CREEK
Drainage fertilization experiment
15N-labelled urea experiment

Appendix 11.8: General layout of drainage ditch network at Wolf Creek, central Alberta. The site was ditched in fall 1987.

Apppendix 11.9. Peat thickness of the experimental tamarack and black spruce area at Wolf Creek, central Alberta.

Fert. treatment	Undrained site	Drained site
Unfert.	124 (12)[1]	119 (13)
N_0PK	121 (8)	119 (9)
N_2PK	117 (11)	114 (14)
N_4PK	124 (4)	116 (9)
Mean	122 (10)	117 (12)

[1] Mean peat depth (cm), with coefficient of variation (%) in parenthesis. Number of observations was 6.

Appendix 11.10: Soil profile descriptions of the drainage and fertilization experiment at Wolf Creek, Central alberta

Appendix 11.10.1: Description of soil profile 1 located on the drained site.

Horizon	Depth cm	Description
Of_1	0 - 8	Green (live) and brown moss.
Of_2	8 - 18	Brown (10YR 4/4 m, unrubbed), dull yellowish orange (10YR 6/3 m, rubbed); moderate, layered; nonsticky; abundant, very fine to medium roots; abrupt boundary; von Post scale of decomposition = 3.
Of_3	18 - 27	Black (10YR 2/1 m, unrubbed), brownish black (10YR 2/3 m, rubbed); moderate, layered; slightly sticky; plentiful, very fine to medium roots; gradual boundary; von Post scale of decomposition = 4.
Om_1	27 - 36	Brownish black (10 YR 2/2 m, unrubbed), brownish black (10 YR 3/2 m, rubbed) moderate, layered; slightly sticky; few, fine to very fine roots; gradual boundary; von Post scale of decomposition = 5.
Om_2	36 - 60	Dark brown (10YR 3/3 m, unrubbed), black (10YR 1.7/1 m, rubbed); moderate, matted; slightly sticky; very few, fine to very fine roots; diffuse boundary; von Post scale of decomposition = 5.

Appendix 11.10.2: Description of soil profile 2 located on the drained site.

Horizon	Depth cm	Description
Of_1	0 - 8.5	Green (live) and brown moss.
Of_2	8.5 - 20	Brownish black (10YR 3/1 m, unrubbed), dark brown (10YR 3/3 m, rubbed); moderate, layered; nonsticky; abundant, very fine to medium roots; abrupt boundary; von Post scale of decomposition = 2.
Of_3	20 -29	Black (10YR 2/1 m, unrubbed), dull yellowish brown (10YR 4/3 m, rubbed); moderate, layered; nosticky; plentiful, very fine to medium roots; gradual boundary; von Post scale of decomposition = 3.
Om_1	29 - 47	Black (10YR 1.7/1 m, unrubbed); brownish black (10YR 2/3 m, rubbed); moderate, layered; slightly sticky; few, very fine to medium roots; gradual boundary; von Post scale of decomposition = 5.
Om_2	47 - 60	Black (10 YR 1.7/1 m, unrubbed), grayish yellow brown (7.5YR 4/2 m, rubbed); moderate, matted; slightly sticky; very few, fine to very fine roots; diffuse boundary; von Post scale of decomposition = 5.

Appendix 11.10.3: Description of soil profile 3 located on the drained site.

Horizon	Depth cm	Description
Of_1	0 - 6	Green (live) and brown moss.
Of_2	6 - 15	Brownish black (10YR 2/2m, unrubbed), dark brown (10YR 3/3 m, rubbed); moderate, layered; nonsticky; abundant, very fine to medium roots; abrupt boundary; von Post scale of decomposition = 2.
Of_3	15 - 23	Black (10YR 1.7/1 m, unrubbed), brownish black 10YR 2/2 m, rubbed); moderate, layered; nosticky; plentiful, very fine to medium roots; gradual boundary; von Post scale of decomposition = 3.

Appendix 11.10.3: continued.

Horizon	Depth cm	Description
Om_1	23 - 30	Brownish black (10YR 2/2 m, unrubbed), dark brown (10YR 3/4 m, rubbed); moderate, layered; slightly sticky; few, fine to very fine medium roots; gradual boundary; von Post scale of decomposition = 5.
Om_2	30 - 60	Dark brown (10YR 3/4 m, unrubbed), brown (10YR 4/6 m, rubbed); moderate, layered; slightly sticky; very few, fine to very fine roots; diffuse boundary; von Post scale of decomposition = 5.

Appendix 11.10.4: Description of soil profile 1 located on the undrained site.

Horizon	Depth cm	Description
Of_1	0 - 5	Green (live) and brown moss.
Of_2	5 - 15	Grayish yellow brown (10YR 5/2m, unrubbed), dull yellowish brown (10YR 5/3 m, rubbed); weak, fibered; nonsticky; abundant, very fine to medium roots; abrupt boundary; von Post scale of decomposition = 3.
Of_3	15 - 27	Dark brown (10YR 3/3 m, unrubbed), brownish black (10YR 2/3 m, rubbed); weak fibered; nosticky; plentiful, very fine to medium roots; abrupt boundary; von Post scale of decomposition = 3.
Of_4	27 - 37	Brownish black (10YR 2/3 m, unrubbed), dark brown (10YR 3/4 m, rubbed); weak matted; nonsticky; abundant, fine to very medium roots; gradual boundary; von Post scale of decomposition = 3.
Om	37 - 60	Brownish black (10YR 2/2 m, unrubbed), brownish gray (10YR 4/1 m, rubbed); weak, matted; slightly sticky; no roots; gradual boundary; von Post scale of decomposition = 4 to 5.

Appendix 11.10.5: Description of soil profile 2 located on the undrained site.

Horizon	Depth cm	Description
Of_1	0 - 6	Green (live) and brown moss.
Of_2	6 - 14	Dull yellowish brown (10YR 5/4 m, unrubbed), dull yellow orange (10YR 6/3 m, rubbed); weak, fibered; nonsticky; abundant, very fine to medium roots; abrupt boundary; von Post scale of decomposition = 3.
Of_3	15 - 24	Dark brown (10YR 3/3 m, unrubbed), grayish yellow brown (10YR 4/2 m, rubbed); weak fibered; nosticky; plentiful, very fine to medium roots; abrupt boundary; von Post scale of decomposition = 3.
Of_4	24 - 34	Brownish black (10YR 3/2 m, unrubbed); brownish black (10YR 2/3 m, rubbed); weak matted; nonsticky; few, fine to very fine roots; gradual boundary; von Post scale of decomposition = 3.
Om	34 - 60	Brownish black (10YR 2/2 m, unrubbed); brown (10YR 4/6 m, rubbed); weak, matted; slightly sticky; no roots; gradual boundary; von Post scale of decomposition = 5.

Appendix II.11: Summary of planned contrasts for foliar and long-shoot responses of tamarack to fertilization treatments within and between drainage levels at Wolf Creek, central Alberta.

		N%[1]		Nc		P%		Pc		K%		Kc		Needle mass		Needle length		Shoot length	
Year	Contrast[2]	t-value	P>t	t-value	P>t	t-value	P>t	t-value	P>t	t-value	P>t	t-value	P>t	t-value	P>t	t-value	P>t	t-value	P>t
1989		Fig. 3.4a				Fig. 3.4d				Fig. 3.4e				Fig. 3.4b,c,e					
	UC vs DC[2,3]	-9.53	<0.001	-4.57	0.002	-5.38	0.001	-3..45	0.009	-4.86	0.001	1.20	0.264	-	-	-	-	-	-
	UC vs UN$_o$PK	-	-	-	-	-4.43	0.002	-3.18	0.013	-2.08	0.071	-0.38	0.714	0.340	0.743	-	-	-	-
	DC vs DN$_o$PK	-	-	-	-	13.9	<0.001	13.4	<0.001	6.71	<0.001	5.50	0.001	2.717	0.026	-	-	-	-
	UN$_o$PK vs DN$_o$PK	-	-	-	-	14.9	<0.001	13.6	<0.001	9.49	<0.001	3.92	0.004	2.038	0.076	-	-	-	-
		Fig. 3.5a				Fig. 3.5c				Fig. 3.5e				Fig. 3.5a,c,e					
	UN$_o$PK vs UN$_2$PK	6.44	<0.001	6.02	<0.001	-2.14	0.053	0.15	0.883	2.22	0.046	9.41	<0.001	2.84	0.015	-	-	-	-
	UN$_o$PK vs UN$_4$PK	5.37	<0.001	7.41	<0.001	-5.21	<0.001	-1.50	0.159	-0.55	0.594	10.9	<0.001	5.59	<0.001	-	-	-	-
	DN$_o$PK vs DN$_2$PK	6.58	<0.001	4.93	<0.001	-11.9	<0.001	-8.95	<0.001	-7.18	<0.001	-7.42	<0.001	0.84	0.416	-	-	-	-
	DN$_o$PK vs DN$_4$PK	11.8	<0.001	8.25	<0.001	-16.8	<0.001	-13.0	<0.001	-11.1	<0.001	-13.2	<0.001	0.82	0.430	-	-	-	-
	UN$_2$PK vs UN$_4$PK	-1.06	0.310	1.39	0.189	-3.06	0.010	-1.65	0.125	-2.77	0.017	1.45	0.172	2.76	0.017	-	-	-	-
	DN$_2$PK vs DN$_4$PK	5.23	<0.001	3.32	0.006	-4.90	<0.001	-4.05	0.002	-3.89	0.002	-5.75	<0.001	-0.026	0.980	-	-	-	-
	UN$_2$PK vs DN$_2$PK	5.87	<0.001	3.28	0.007	4.59	0.001	3.35	0.006	1.51	0.156	0.71	0.490	-0.72	0.488	-	-	-	-
	UN$_4$PK vs DN$_4$PK	12.2	<0.001	5.21	<0.001	2.76	0.017	0.95	0.361	0.39	0.702	-6.49	<0.001	-3.50	0.004	-	-	-	-
1990		Fig. 3.4a				Fig. 3.4c				Fig. 3.4e				Fig. 3.4b,c,e					
	UC vs DC	-9.61	<0.001	-4.79	0.001	-4.47	0.002	-1.74	0.121	-1.76	0.117	1.09	0.100	-2.36	0.046	-4.64	0.002	-1.97	0.085
	UC vs UN$_o$PK	-	-	-	-	-12.7	<0.001	-1.66	0.135	-1.38	0.205	-	-	-	-	-	-	-	-
	DC vs DN$_o$PK	-	-	-	-	32.1	<0.001	5.26	0.001	4.02	0.004	-	-	-	-	-	-	-	-
	UN$_o$PK vs DN$_o$PK	-	-	-	-	23.9	<0.001	5.34	0.001	4.39	0.002	-	-	-	-	-	-	-	-
		Fig. 3.5a				Fig. 3.5c				Fig. 3.5e				Fig. 3.5a,c,e					
	UN$_o$PK vs UN$_2$PK	2.40	0.043	2.49	0.028	-3.34	0.006	-0.13	0.900	-0.56	0.588	-	-	2.63	0.022	1.292	0.221	0.910	0.381
	UN$_o$PK vs UN$_4$PK	2.81	0.016	2.66	0.021	-3.99	0.002	-0.48	0.643	-1.04	0.319	-	-	2.80	0.016	1.482	0.164	0.122	0.905
	DN$_o$PK vs DN$_2$PK	0.39	0.704	2.36	0.036	-8.66	0.0001	-2.78	0.017	-2.40	0.034	-	-	2.05	0.063	2.502	0.028	3.412	0.005
	DN$_o$PK vs DN$_4$PK	5.06	0.0001	6.03	0.0001	-11.0	0.0001	-3.93	0.002	-4.39	0.001	-	-	3.49	0.004	1.343	0.204	0.052	0.959
	UN$_2$PK vs UN$_4$PK	0.41	0.691	0.17	0.871	-0.65	0.529	-0.35	0.735	-0.48	0.638	-	-	0.17	0.871	0.190	0.852	-0.787	0.446
	DN$_2$PK vs DN$_4$PK	4.67	0.001	3.67	0.003	-2.37	0.035	-1.15	0.273	-1.99	0.070	-	-	1.45	0.174	-1.159	0.269	-3.359	0.006
	UN$_2$PK vs DN$_2$PK	6.51	0.0001	4.64	0.001	2.72	0.019	2.56	0.025	2.54	0.026	-	-	2.36	0.036	3.198	0.008	5.931	0.0001
	UN$_4$PK vs DN$_4$PK	10.9	0.0001	8.15	0.0001	1.00	0.338	1.76	0.104	1.03	0.325	-	-	3.64	0.003	1.849	0.089	3.359	0.006

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[1] N% - foliar N concentration, Nc - foliar N content, P% - foliar P concentration, Pc - foliar P content, K% - foliar K concentration, Kc - foliar K content.

[2] Degrees of freedom for contrast is 1 and for the error mean squares pertaining to figures 3.3 and 3.4 are respectively 8 and 12; values for EMS are given in Table 3.4.

[3] U - undrained, D - drained, C - unfertilized.

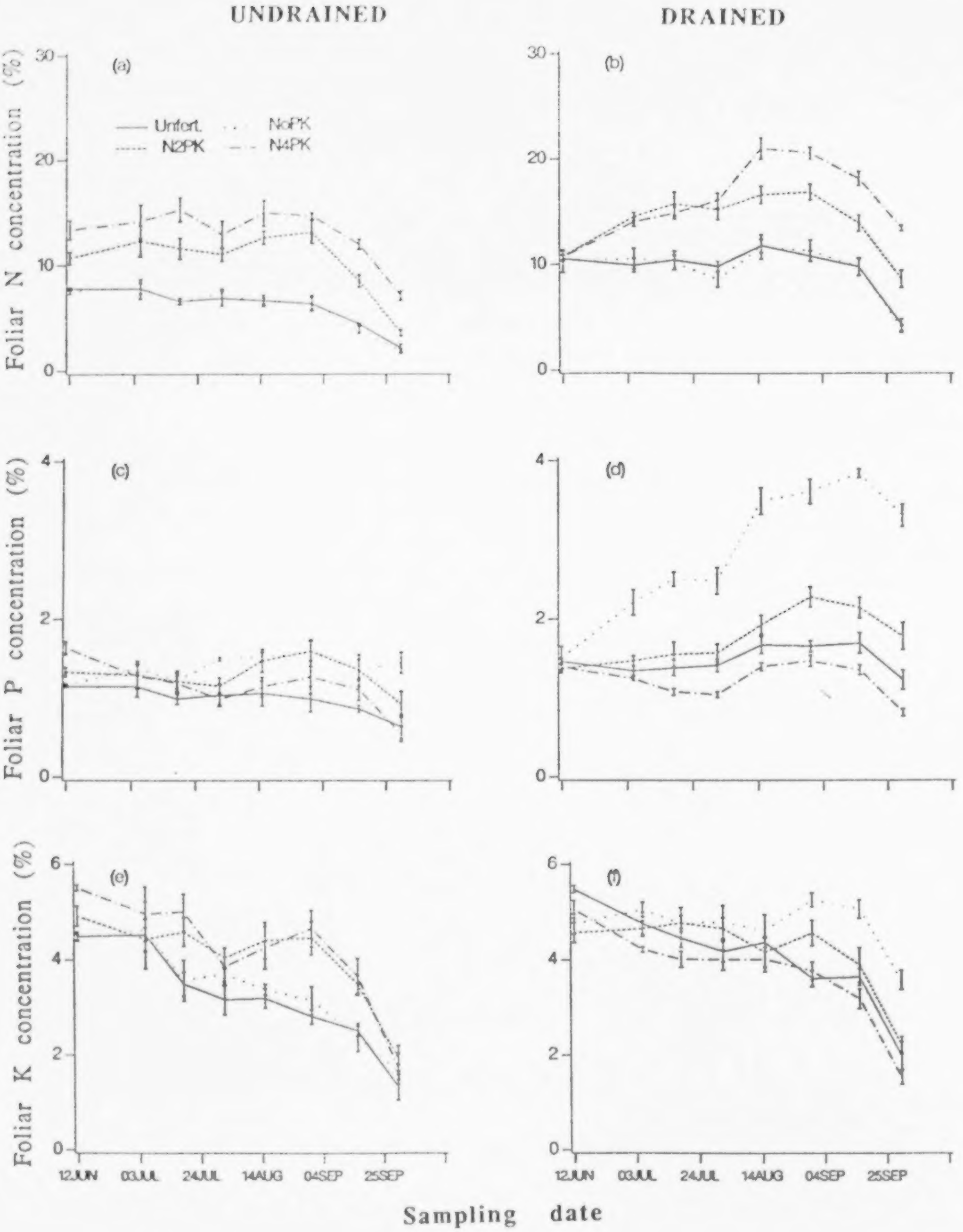
Appendix 11.12 Summary of planned contrasts for foliar responses black spruce fertilization treatments within and between drainage levels at Wolf Creek, central Alberta.

		N%[1]		Nc		P%		K%		Kc		Foliar mass	
Year	Contrast[2]	t-value	P>t	t-value	P>t	t-value	P>t	t-value	P>t	t-value	P>t	t-value	P>t
1989		Fig. 3.4b				Fig. 3.4d		Fig. 3.4f				Fig. 3.4b,d,f	
	UC vs DC	-3.64	0.007	-	-	-3.30	0.011	-	-	-2.29	0.051	1.20	0.264
	UC vs UN$_o$PK	-	-	-	-	-1.65	0.137	-2.80	0.023	-	-	-	-
	DC vs DN$_o$PK	-	-	-	-	4.95	0.001	2.02	0.078	-	-	-	-
	UN$_o$PK vs DN$_o$PK	-	-	-	-	6.61	<0.001	0.47	0.653	-	-	-	-
		Fig. 3.5b				Fig. 3.5d						Fig. 3.5b,d,f	
	UN$_o$PK vs UN$_2$PK[3]	2.77	0.017	1.97	0.072	0.32	0.752	-	-	-	-	0.84	0.416
	UN$_o$PK vs UN$_4$PK	3.25	0.007	2.40	0.034	-1.70	0.166	-	-	-	-	0.61	0.556
	DN$_o$PK vs DN$_2$PK	3.55	0.004	2.47	0.030	-2.10	0.058	-	-	-	-	1.02	0.328
	DN$_o$PK vs DN$_4$PK	4.68	0.001	3.37	0.006	-3.31	0.006	-	-	-	-	1.47	0.168
	UN$_2$PK vs UN$_4$PK	0.48	0.642	0.43	0.678	-2.02	0.066	-	-	-	-	-0.24	0.816
	DN$_2$PK vs DN$_4$PK	1.13	0.282	0.90	0.386	-1.21	0.249	-	-	-	-	0.45	0.663
	UN$_2$PK vs DN$_2$PK	1.95	0.075	0.68	0.509	3.80	0.003	-	-	-	-	-0.32	0.751
	UN$_4$PK vs DN$_4$PK	2.60	0.023	1.15	0.271	4.60	0.001	-	-	-	-	0.36	0.725
1990		Fig. 3.4b				Fig. 3.4d							
	UC vs DC	-6.13	<0.001	-1.27	0.241	-3.13	0.014	-2.46	0.040	-	-	-	-
		Fig. 3.5d				Fig. 3.5e							
	UN$_o$PK vs DN$_2$PK	2.66	0.021	0.067	0.948	0.20	0.843	-	-	-	-	-	-
	UN$_o$PK vs UN$_4$PK	5.06	0.0001	1.44	0.176	0.91	0.380	-	-	-	-	-	-
	DN$_o$PK vs DN$_2$PK	2.81	0.016	1.96	0.074	-3.35	0.006	-	-	-	-	-	-
	DN$_o$PK vs DN$_4$PK	3.16	0.008	2.43	0.032	-3.45	0.005	-	-	-	-	-	-
	UN$_2$PK vs UN$_4$PK	2.39	0.034	1.37	0.195	0.71	0.492	-	-	-	-	-	-
	DN$_2$PK vs DN$_4$PK	0.35	0.736	0.47	0.646	-0.10	0.921	-	-	-	-	-	-
	UN$_2$PK vs DN$_2$PK	3.44	0.005	3.26	0.007	1.62	0.131	-	-	-	-	-	-
	UN$_4$PK vs DN$_4$PK	1.39	0.189	2.36	0.036	0.81	0.433	-	-	-	-	-	-

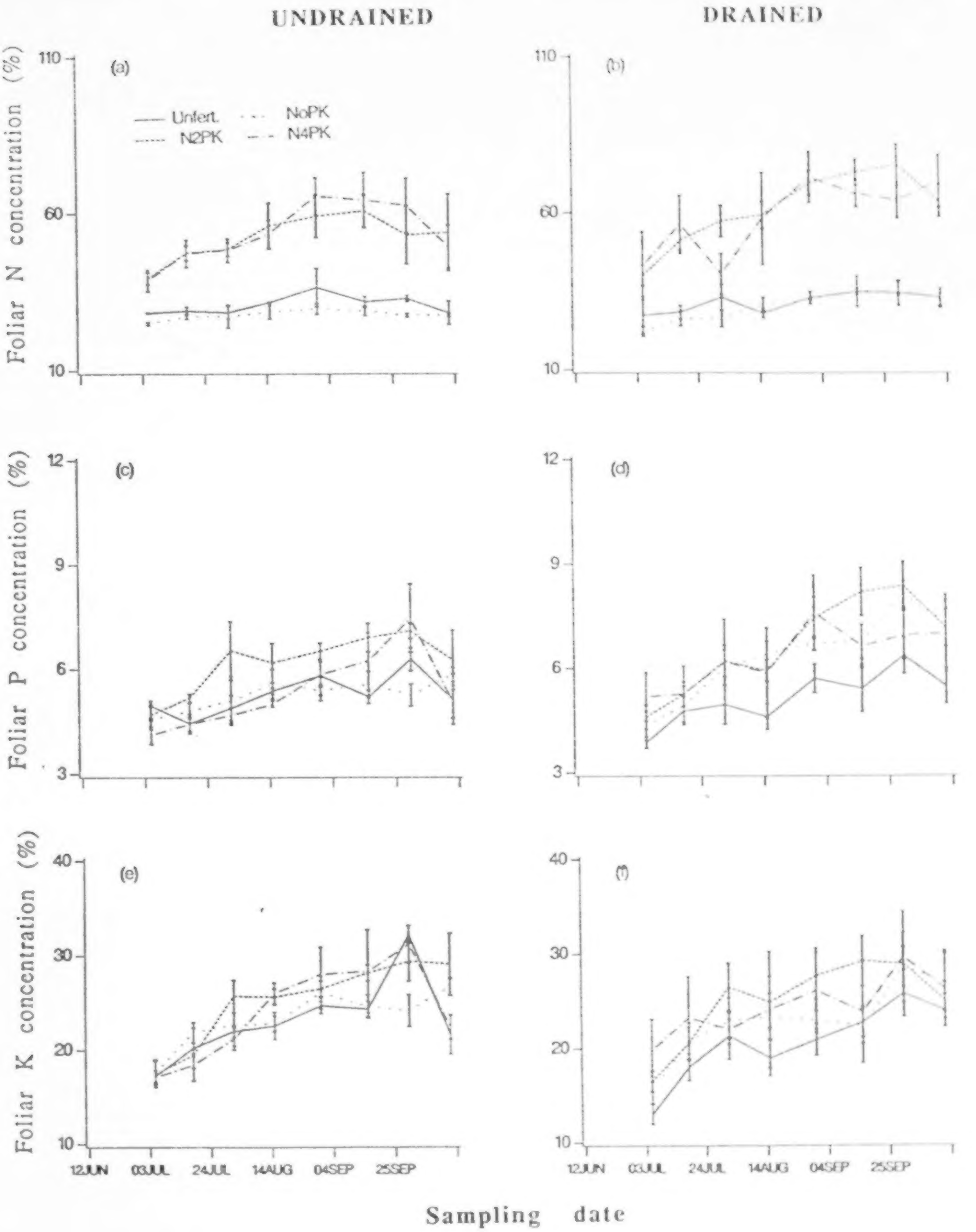
[1] N% - foliar N concentration, Nc - foliar N content, P% - foliar P concentration, Pc - foliar P content, K% - foliar K concentration, Kc - foliar K content.

[2] Degrees of freedom for contrast is 1 and for the error mean squares pertaining to figures 3.3 and 3.4 are respectively 8 and 12; values for EMS are given in Table 3.4.

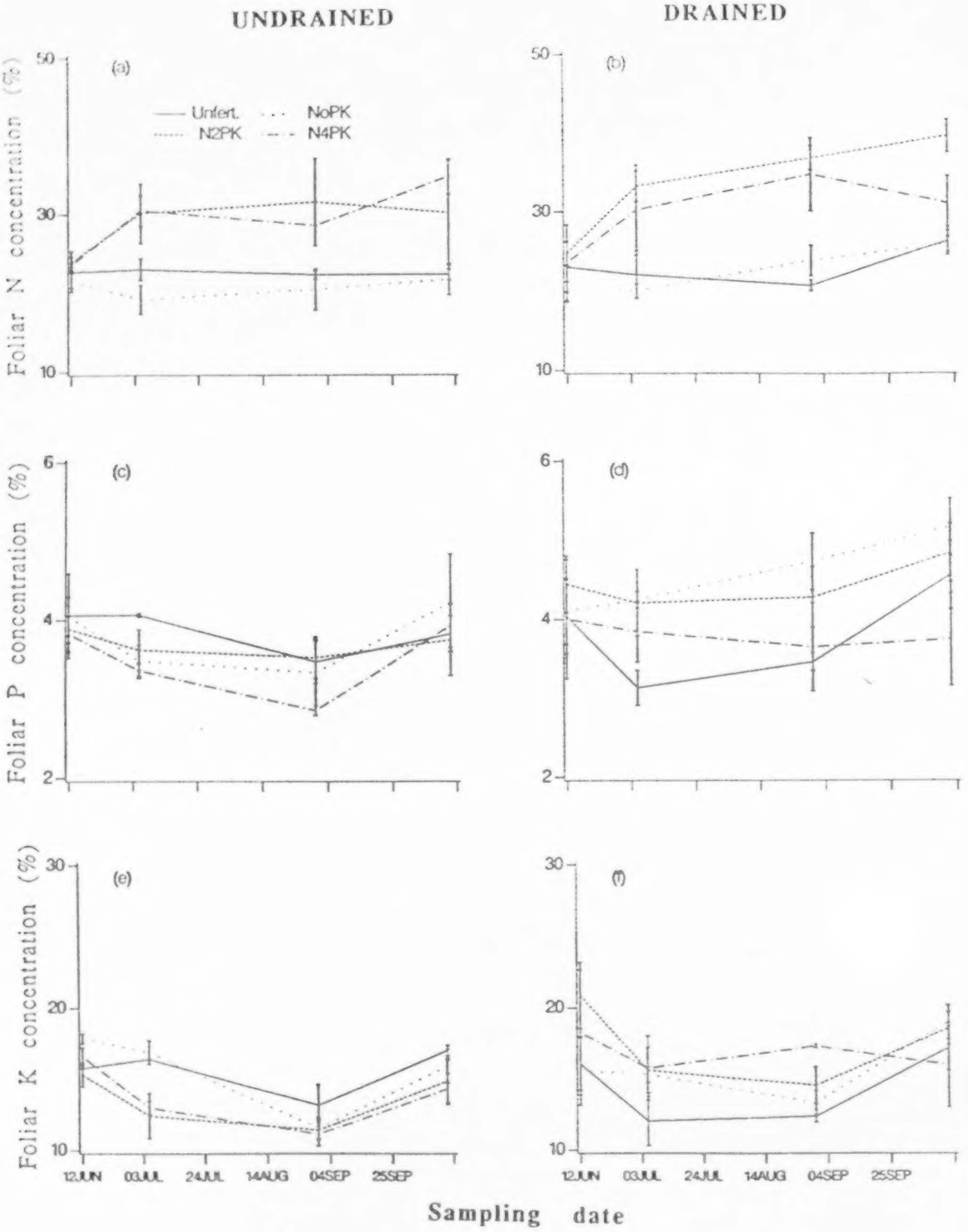
[3] U - undrained, D - drained, C - unfertilized.



Appendix 11.13: Seasonal response patterns for nitrogen, phosphorus and potassium contents in short-shoot needles of undrained and drained tamarack. Mean values ± SE are based on 2 to 3 samples on the undrained site and 4 to 6 samples on the drained site.



Appendix 11.14: Seasonal response patterns for nitrogen, phosphorus and potassium contents in current-year needles of undrained and drained black spruce as defined in Appendix 11.13.



Appendix 11.15: Seasonal response patterns for nitrogen, phosphorus and potassium contents in one-year-old needles of undrained and drained black spruce as defined in Appendix 11.13.

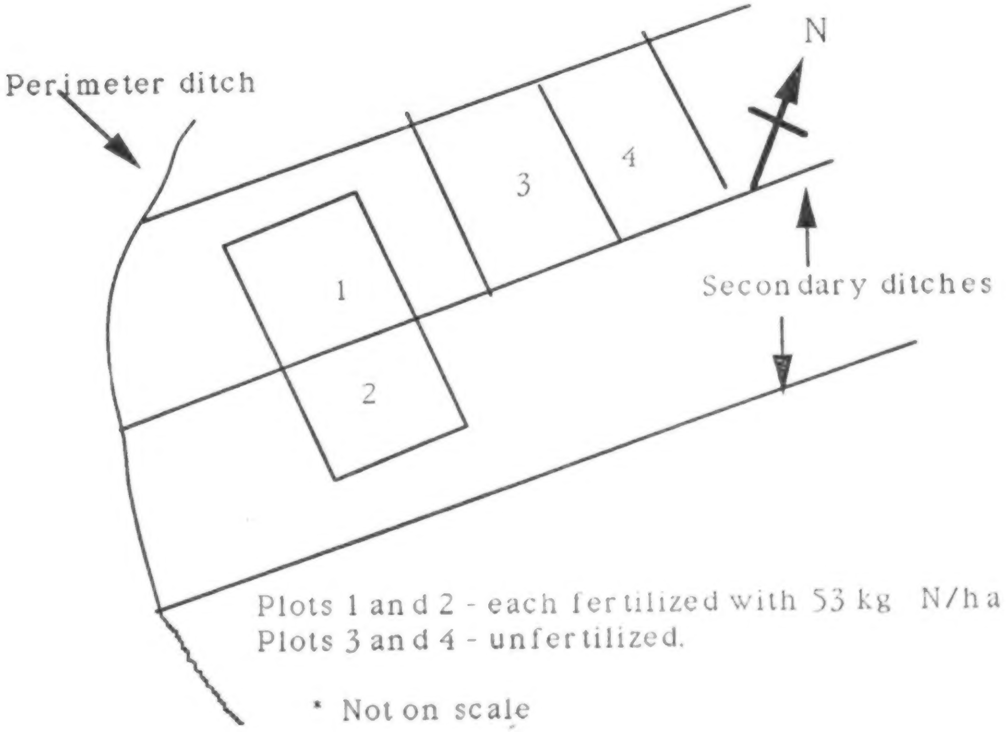

Perimeter ditch
N
1
2
3
4
Secondary ditches
Plots 1 and 2 - each fertilized with 53 kg N/ha
Plots 3 and 4 - unfertilized.
* Not on scale

Figure 11.16: Layout of plots for ^{15}N-labelled urea experiment at Wolf Creek, central Alberta.

Appendix 11.17: Summary of t-test for the effect of crown position on foliar attributes of current, one-, two-, three- and six-year plus older needles of ^{15}N-fertilized black spruce sampled on 31 August 1989 (thirteen weeks after urea application) at Wolf Creek, central Alberta.

Foliar attrib.	1989		
	U vs M[a]	U vs L	M vs L
	Current needles		
Needle mass	0.01[b]	<0.01	n s
N concentration	n s	0.07	n s
N content	n s	<0.01	n s
%NDFF	0.02	n s	n s
^{15}N content	0.08	n s	n s
	One-year-old needles		
Needle mass	<0.01	<0.01	n s
N concentration	n s	n s	n s
N content	<0.01	<0.01	n s
%NDFF	n s	n s	n s
^{15}N content	n s	n s	n s
	three-year-old needles		
Needle mass	<0.01	n s	n s
N concentration	n s	n s	n s
N content	<0.01	0.02	n s
%NDFF	n s	n s	n s
^{15}N content	n s	n s	n s
	six-year and older needles		
Needle mass	0.10	n s	n s
N concentration	n s	0.07	0.07
N content	n s	n s	n s
%NDFF	0.02	n s	n s
^{15}N content	n s	n s	n s

[a] Crown positions: U - upper, M - middle and L lower;

[b] P>t

Appendix 11.18: Effect of needle age on foliar attributes of ^{15}N - labelled urea fertilized black spruce in relation to crown position on 31 August 1989 (thirteen weeks after urea application) at Wolf Creek, central Alberta.

Foliar attribute	Crown position	ANOVA of needle age[1]		
		MS	Error	P>F
Needle mass	Upper	0.293	0.44	n s
	Middle	1.034	0.276	0.02
	Lower	0.607	0.323	n s
N concn.	Upper	0.187	0.0061	<0.01
	Middle	0.419	0.0057	<0.01
	Lower	0.190	0.009	<0.01
N content	Upper	320.5	24.5	<0.01
	Middle	533.1	23.7	<0.01
	Lower	278.3	23.2	<0.01
%NDFF	Upper	8.11	1.58	<0.01
	Middle	27.1	3.78	<0.01
	Lower	31.1	8.05	0.02
^{15}N content	Upper	2.42	0.198	<0.01
	Middle	7.63	0.628	<0.01
	Lower	7.33	0.966	<0.01

[1] Degrees of freedom for age and error in 1989 for each crown position were respectively: upper - 6 and 55, middle - 3 and 35, and lower 3 and 31.

MS - mean square.

Appendix 11.19: Mean characteristics of trees sampled for determination of the aboveground component biomass equations at Wolf Creek, central Alberta.

		Black spruce	
	Tamarack	< 2 m height	> 2 m height
Number of trees	36	22	26
Dbh (cm)	5.50 (1.4 - 11.4)[1]	2.17 (1.5 - 3.1)[2]	5.74 (1.9 - 11.7)
Total height (m)	5.63 (0.88-8.28)	1.37 (0.65-1.78)	4.74 (1.96-7.97)
Foliage mass (kg)	0.30 (0.02-1.35)	0.31 (0.07-0.33)	1.69 (0.31-6.12)
Stemwood (kg)	4.60 (0.66-15.6)	0.16 (0.02-0.21)	3.24 (0.23-13.9)
Branchwood (kg)	1.12 (0.08-5.40)	0.16 (0.03-0.18)	1.44 (0.19-7.18)
Stembark (kg)	0.82 (0.16-2.29)	0.09 (0.02-0.07)	0.59 (0.04-2.79)

[1] Mean with the range in parenthesis.

[2] basal diameter measured at 0.1 m aboveground.

Appendix 11.20: Total N and ^{15}N status of other components of tamarack and black spruce on a minerotrophic peatland fertilized with ^{15}N-labelled urea at the dose of 53 kg N.ha^{-1} at Wolf Creek, central Alberta. Urea was applied on 1 June 1989.

	Crown	31 August 1989		2 September 1990	
Species	posit.	N%[a]	%NDFF	N%	%NDFF
Tamarack					
twigs	U[b]	0.56[c]	1.59	0.63	1.96
		(0.03)	(0.07)	(0.01)	(0.13)
	M	0.58	2.14	0.57	1.73
		(0.04)	(0.28)	(0.01)	(0.13)
	L	0.61	1.56	0.60	1.67
		(0.01)	(0.11)	(0.01)	(0.18)
stembark		0.34	3.26	0.27	1.70
		(0.01)	(0.52)	(0.02)	(0.05)
roots		0.35	8.57	0.35	4.96
		(0.01)	(2.02)	(0.06)	(1.21)
B. spruce					
twigs					
C[d]	U	0.78	4.72	0.92	5.65
		(0.02)	(1.29)	(0.01)	(0.23)
C+1	U	nd[e]	nd	0.64	5.43
				(0.02)	(0.18)
rest	U	0.55	2.54	0.57	3.55
		(0.09)	(0.75)	(0.01)	(0.10)
C	M	0.78	4.70	0.65	8.28
		(0.03)	(0.66)	(0.00)	(1.53)
rest	M	0.49	3.06	0.57	3.55
		(0.04)	(0.18)	(0.01)	(0.10)

[a] N% - total nitrogen (% dry wt.); %NDFF - percent of nitrogen derived from fertilizer;

[b] U- upper crown position, M - mid crown position, and L - lower crown position;

[c] mean of two plots, SE in parenthesis;

[d] C - current twigs, C+1 - one year old twigs, C+2 - two year old twigs, and rest - three year and older twigs.

[e] nd - not determined.

Appendix 11.20: continued.

Species	Crown posit.	1989 N%[a]	1989 %NDFF	1990 N%	1990 %NDFF
Black spruce twigs					
	C[d] L[b]	0.86[c]	6.85	0.74	6.68
		(0.03)	(0.87)	(0.04)	(0.18)
	rest L	0.61	4.45	0.45	5.09
		(0.06)	(0.80)	(0.02)	(0.36)
stembark		0.22	3.00	0.23	2.77
		(0.02)	(0.05)	(0.02)	(0.15)
roots		0.41	7.09	0.33	5.34
		(0.06)	(1.21)	(0.05)	(0.96)

Appendix 11.21: Total N% and ^{15}N status of aboveground components of understory species in a tamarack/black spruce mixed stand on a minerotrophic peatland fertilized with ^{15}N-labelled urea at the dose of 53 kg N ha^{-1}, at Wolf Creek, central Alberta. Urea was applied on 1 June 1989.

Species		31 August 1989 N[a]	^{15}N exc.	NDFF	2 September 1990 N	^{15}N exc.	NDFF
		%					
Carex spp		2.07[b]	0.259	9.32	1.33	0.075	2.73
		(0.25)	(0.095)	(3.42)	(0.23)	(0.075)	(0.56)
Betula pumila							
	foliage	2.62	0.242	8.71	2.49	0.121	4.37
		(0.15)	(0.047)	(1.68)	(0.02)	(0.026)	(0.92)
	branches/ stems	0.91	0.208	7.48	0.94	0.096	3.46
		(0.04)	(0.060)	(2.16)	(0.01)	(0.022)	(0.78)
Ledum groenlandicum							
	foliage	1.68	0.540	19.5	1.48	0.412	14.9
		(0.06)	(0.133)	(4.78)	(0.13)	(0.056)	(2.03)
	branches/ stems	0.75	0.435	15.7	0.62	0.360	13.0
		(0.04)	(0.068)	(2.40)	(0.03)	(0.072)	(2.60)
Others	foliage	2.07	0.253	9.13	1.84	0.095	3.43
		(0.07)	(0.023)	(0.84)	-	-	-
	branches/ stems	0.94	0.188	6.78	0.80	0.070	2.19
		(0.07)	(0.043)	(1.56)	-	-	-

[a] N% - total nitrogen (% dry wt.), ^{15}Nexc - ^{15}N atom percent excess, and NDFF - percent of nitrogen derived from fertilizer.

[b] Mean of two samples followed by the standard error in parentheses.

Appendix 11.22: Ammonia volatilization following urea application onto ^{15}N experimental plots at Wolf Creek, central Alberta.

11.22.1 Introduction

When urea fertilizer is added to forest soil, it is usually hydrolysed to ammonium carbonate by soil urease. The rapid accumulation of ammonium and ammonia and a corresponding rise in pH lead to gaseous loss of nitrogen as ammonia (Marshall and DeBell (1980). The factors involved in this process appear to be numerous (Macrae and Ancajas 1970) and may vary from place to place. Hence the magnitude of ammonia loss from forest soils vary widely (Nason *et al.* 1988). The present substudy was undertaken in order to estimate gaseous loss of applied N through ammonia volatilization from a forest floor under tamarack/black spruce stand on a drained (fall 1987) minerotrophic peatland.

11.22.2 Materials and Methods

Ammonia volatilization was measured by the microplot procedure using the NH_3 sorber technique described by Marshall and DeBell (1980). Four microplots were set up in each of the four (i.e. two unfertilized - control and two fertilized) plots. Each microplot was made up of an open ended steel cylinder of 20 cm internal diameter and 30 cm height (base) and a sorber chamber constructed from plastic pipe (20 cm i.d. and 15 cm tall). The sorber chamber housed two horizontal polyfoam sorber discs (20 cm diameter and 2 cm thick) held in place by two 5 mm diameter aluminum pins driven through the centre of the sorber chamber at 5 cm and 10 cm from the bottom. NH_3 evolved from the soil was captured by the lower sorber, ambient NH_3 by upper sorber. The sorber was sheltered from throughfall by an inverted, disposable aluminum pie plate (Nason *et al.* 1988). Contamination of discs was prevented by adopting the procedure suggested by Marshall and DeBell (1980).

Steel cylinders were installed by cutting into the peat during summer 1988. The cylinders protruded 2 to 3 cm above the surface of live moss for fitting sorber chambers. Before fertilization all herbaceous plants within each microplot were removed by cutting at the surface of live moss. Fertilizer was applied as described in section 8.2.2. Two sorber chambers were fitted to two steel cylinders and secured in place by rubber band (3 cm wide). The sorber disks (polyfoams) charged by soaking in 0.75 M phosphoric acid in 2.5% glycerol and allowing excess solution to drain under gravity (Nason *et al.* 1988) were placed in the sorber chambers of two microplots in each plot. Sorber discs in each sorber chamber were replaced by fresh sorber discs every 48 or 72 h for a period of 16 days following fertilizer application. After each replacement of a sorber disc sorber chambers were transfered to a second set of steel cylinders within each plot. All retrieved sorber disks were stored at -20 °C for future chemical analysis.

In the laboratory, disk sorbers were thawed and sorbed NH_3 was extracted by being rinsed and squeezed dry with 4 x 100 mL of deionized water. Extracts were poured into the volumetric flask and made up to volume with deionized water. NH_4^+-N in the extracts was determined by automated analysis (Technicon Instruments 1977).

11.22.3 Results

Periodical loss of fertilizer N through ammonia volatilization from forest floor of a mixed tamarack/black spruce stand following addition of urea fertilizer was as follows:

	Period (days)					
Plot	0 - 3	3 - 5	5 - 9	9 - 13	13 -16	Total
	Ammonia loss (kg N.ha^{-1})					
1	1.757[a]	1.534	2.172	0.321	0.093	5.577
2	0.548	0.639	1.908	0.419	0.109	3.622
Mean	1.152	1.086	2.040	0.370	0.100	4.599

[a] Ammonia loss less control (unfertilized)

Ambient and soil temperatures during the first seven days following fertilizer application are summarized below. During the first two weeks following urea application, rainfall totalled 56 mm. The first rainfall event which occurred on 9 June (urea applied on 1 June) accounted for 73% of the total rainfall.

Day	1	2	3	4	5	6	7
Temp. (°C)							
Ambient[a]	18.6[b] (24--1.1)	10.6 (22--1.1)	10.8 (23--1.1)	14.2 (29--1.1)	15.3 (31--0.6)	11.9 (21-3)	10.0 (22--2)
Soil	37.9[c] (3.7)	37.7 (0.47)	35.7 (12)	35.2 (0.30)	31.6 (2.4)	-	-

[a] Ambient temperature and precipitation were recorded at the metrological station established at the study area by Dr. G.R. Hillman (see Figure 3.2);

[b] Daily mean followed by minimum and maximum in parentheses.

[c] Mean of at least 10 observations followed by standard deviation in parentheses. Temperature was measured at random within each plot, within 1 and 2 cm below the surface of live moss with a thermocouple between 1200 and 1400 h.

11.22.4. References

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